Landscape utilisation by an introduced pack of African wild dogs (*Lycaon pictus*) in eastern Botswana.

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PLAGIARISM DECLARATION

I know that plagiarism is wrong. Plagiarism is using another's work and pretending that it is one's own. I have used Conservation Biology as the convention for citing and referencing. Each significant contribution to, and quotation in, this project from the work, or works of other people, has been attributed, cited and referenced. This project is my own work, I have not allowed and will not allow, anyone to copy my work with the intention of passing it off as his or her own. I acknowledge that copying someone else's work, or parts of it, is wrong and I declare that this is my own work.

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ABSTRACT

African wild dogs (*Lycaon pictus*) are one of the most endangered carnivores in southern Africa. Direct persecution, prey decline and habitat loss and fragmentation all contributed to a rapid decline in this species' population size and distribution during the 20th century. Following a thorough population viability analysis in the late 1990s the decision was taken to manage the South African population as a metapopulation. This involved the reintroduction of packs to small, fenced protected areas and the subsequent transfer of individuals or small groups between reserves to avoid inbreeding. A key component of successful metapopulation management is post-release monitoring to provide data on the determinants of reintroduction success and failure, particularly when establishing new populations. This study aimed to provide information on the post-release behaviour and movements of a pack of eight African wild dogs introduced to the Northern Tuli Game Reserve in eastern Botswana in February 2017. Two individuals from the introduced pack were fitted with GPS collars. A total of 933 GPS locations were recorded between February 2017 and October 2017. Movement data was used to analyse home range, habitat resistance and resource utilisation by this pack across a range of spatial and temporal scales. Monthly 95% kernel density estimations revealed a mean home range of 330.02 km^2. A reduction in home range size to 37% of the average monthly 95% kernel density estimations revealed that the pack commenced denning in May 2017. However, this denning attempt failed, as shown by the home range size increasing only a month after it initially contracted, which is less than the expected contraction period required to produce a successful litter. Habitat resistance analysis revealed that the pack readily crossed fences but not rivers, with the Limpopo river serving as a very hard barrier that consistently deflected pack movement parallel to its course. Resource utilisation functions showed a preference for sites far from riverine areas, with low elevation and rough and rocky terrain. I propose that this may reflect a predator avoidance pattern, with lions (*Panthera leo*) in particular preferring riverine habitat with a less rough terrain in this area. The persistence of this pack in the landscape nine months post-release indicates that this reintroduction has been a partial success. Large perennial rivers provide important barriers to the movement of this pack and may thus be important for mitigating local human-wild dog conflict. Fences, however, were readily traversed and therefore communities outside of fenced areas are likely to experience conflict with this pack and any future packs re-introduced to this area.

Keywords: African wild dog, reintroduction, movement analysis, metapopulation, human-wildlife conflict.

1. INTRODUCTION

1.1 Carnivore Decline

The order Carnivora contains some of the most iconic, yet endangered species in the world (Ripple *et al*., 2014; Rosenblatt *et al.,* 2014; Wolf & Ripple, 2016). In the last two centuries alone, there have been significant declines in both abundance and distribution of many carnivore species, mainly as a result of human activities (Treves & Karanth, 2003; Ripple *et al.,* 2014). As wide-ranging, long-lived and often territorial animals which are dependent upon meat, carnivores have been negatively impacted by human-induced habitat loss (Treves & Karanth, 2003; Ripple *et al.,* 2014), over-exploitation (Chapron *et al.*, 2008; Packer *et al.*, 2011), direct persecution (Woodroffe *et al*., 2005; Fraser-Celin *et al.,* 2017) and prey reduction (Wolf & Ripple, 2016). This combination of threats is known as "human-carnivore conflict" (Rosenblatt *et al.,* 2014).

1.1.1 Human-carnivore conflict

Human-carnivore conflict poses one of the greatest threats to carnivore survival today (Treves & Karanth, 2003; Woodroffe *et al.,* 2005; Hayward & Somers, 2009). It increases the vulnerability of many naturally-rare carnivore species to stochastic events such as disease outbreak, which can reduce population sizes and potentially lead to extinction (Treves & Karanth, 2003; Hayward & Somers, 2009; Ripple *et al*., 2014).

Lethal control

Lethal control, otherwise known as "retributive killing" (Woodroffe *et al*., 2005) is the most common result of livestock depredation by carnivores (Thirgood *et al*., 2005; Treves & Naughton-Treves, 2005; Gusset *et al.,* 2009; Fraser-Celin *et al.,* 2017). Both the wide-ranging nature of carnivores and the increasing encroachment of pastoralism into carnivore-dominated landscapes means that carnivores are more likely to come in to contact with domestic livestock. Due to their poor "anti-predator behaviour" (Thirgood *et al*., 2005) livestock, such as goats, sheep and cattle, are easy prey for many carnivores, as shown by pumas (*Puma concolor*) predating upon cattle in South America and bears (*Ursus spp*.) predating upon sheep in North America (Treves & Karanth 2003; Fraser-Celin *et al.,* 2017). The loss of livestock can have significant negative impacts on human livelihoods and therefore many communities feel the only way to remove the threat of livestock depredation is to use lethal control – even when there is no direct proof of the carnivore killing the livestock (Treves & Naughton-Treves, 2005; Woodroffe *et al.,* 2005). Many conservationists have suggested that lethal control is the greatest threat facing carnivores today and will increase as the competition between

wildlife conservation and human development intensifies (Treves & Karanth, 2003; Woodroffe *et al.,* 2005; Hayward & Somers, 2009; Packer *et al.,* 2011; Fraser-Celin *et al.,* 2017).

1.1.2 Over-exploitation

Over-exploitation can occur through sport and trophy hunting as well as poaching and bushmeat harvesting (Goodrich *et al.,* 2008; Packer *et al.*, 2011; Rosenblatt *et al.,* 2014; Robinson *et al.,* 2015). Packer *et al.* (2011) studied the impact of sport hunting on large, charismatic carnivores such as lions (*Panthera leo*) and leopards (*Panthera pardus*) in Tanzania and found that unsustainable levels of trophy hunting had reduced the abundance of these two species both inside and outside of hunting concessions. There is clearly a need for sustainable, well-managed and monitored quotas and age limits to ensure that trophy hunting can still contribute to economies and conservation without damaging ecosystems and threatening local populations (Rosenblatt *et al.*, 2014).

Poaching and bushmeat harvesting also pose serious, exploitative threats to carnivores worldwide. Both Goodrich *et al.* (2008) and Robinson *et al.* (2015) found that poaching was responsible for the majority of Amur tiger (*Panthera tigris altaica*) mortality worldwide. Snares, which are set by bushmeat harvesters intending to trap herbivores such as ungulates, can trap carnivores which frequent ungulate-dense areas in search of food (Becker *et al.,* 2013). The effects of this indirect trapping of carnivores are not yet well understood. However, Becker *et al.*'s (2013) observations in Luangwa Valley in Zambia showed that lions and African wild dogs (*Lycaon pictus*) were particularly susceptible to entrapment in snares due to their wide-ranging behaviours. It is important to note that because they are illegal activities in many areas, the impacts of poaching and bushmeat harvesting are difficult to quantify. Consequently, while we know that they pose a threat to carnivores, the extent and intensity of this threat is still unclear.

1.1.3 Habitat loss

Human-induced habitat loss can take the form of habitat fragmentation, transformation, degradation and destruction and has adversely impacted most species on the planet (Brooks *et al.,* 2002; Fahrig, 2003). Carnivores have been particularly badly affected due to their wide-ranging behaviour and have consequently suffered significant range contractions (Treves & Karanth, 2003; Davies-Mostert *et al*., 2009; Kelly & Silver, 2009). Ripple *et al*. (2014) studied 17 different carnivore species and found that on average they now occupied only 47% of their historical ranges. While there have been some attempts to prevent the complete loss of habitat by developing both unfenced and fenced protected areas, these are often insufficient in extent and fences invariably restrict carnivore ranging, confining them to, at times, suboptimal habitat (Hayward & Kerley, 2009; Cozzi *et al*., 2013). The encroachment of pastoralists, particularly during droughts, into previously carnivore dominated

landscapes also brings about the possibility of increasing transmission of diseases such as rabies from domesticated dogs (*Canis lupus familiaris*) (Chaudhary, 2016). Habitat loss has also adversely impacted many ungulate species which carnivores predate upon (Wolf & Ripple, 2016).

1.1.4 Prey decline

Carnivores are most commonly "obligate-meat eaters" (Ripple *et al.,* 2014), meaning they require significant quantities of meat for their metabolic processes (Ripple *et al*., 2014). On average, 10 000 kg of prey biomass supports around 90 kg of large carnivore biomass regardless of species (Carbone & Gittleman, 2002; Wolf & Ripple, 2016). However, the prey species are not immune to human-wildlife conflict and have also suffered losses in abundance and distribution as a result of habitat loss and over-exploitation. Such a loss of prey causes "bottom-up limitation" (Hayward & Somers, 2009) for many carnivore species as they no longer have access to sufficient quantities of their preferred food. Wolf & Ripple (2016) suggested that the main reason for carnivore decline was a lack of prey, stating that at least 40% of the prey species for the endangered Ethiopian wolf (*Canis simensis*) and the clouded leopard (*Neofelis diardi*) were threatened.

1.1.5 Emerging conflicts

Human-carnivore conflict is a complex combination of biological, socio-economic and political factors. It is an increasingly serious threat to carnivores and has already led to significant declines in abundance and distribution of many iconic species (Treves & Karanth, 2003; Woodroffe *et al*., 2005; Hayward & Somers, 2009). In addition to the threats mentioned above, there are a number of emerging indirect threats which could potentially have serious impacts on carnivores – of which climate change is the most pertinent. As a global, wicked problem, the impact of climate change on carnivores is only beginning to be understood (Cardillo *et al*., 2004; Packer *et al*., 2011; Khorozyan *et al.,* 2015). Carnivores are undeniably important both economically and ecologically, and thus we have an incentive and a responsibility to protect and conserve them.

1.2 Importance of carnivores

Carnivores can hold extrinsic (Sillero-Zubiri & Laurenson, 2001), existence (Macdonald, 2001) and intrinsic value (Ray, 2005). The extrinsic value of carnivores lies in their economic and ecological importance (Sillero-Zubiri & Laurenson, 2001), yet many people place a disproportionately large amount of existence value on large, charismatic carnivores too (Macdonald, 2001). An existence value suggests that humans can value carnivores just for existing, even if the person placing value upon the species may never see or come in to contact with it (Macdonald, 2001). Furthermore, just

like every other species in the world, carnivores hold an intrinsic value; they have a right to exist and their value should not have to be justified (Ray, 2005).

Economic importance

Economically speaking, carnivores are extremely important. Carnivores such as leopard, tiger (*Panthera tigris*) and jaguar (*Panthera onca*) can provide direct economic benefits to humans through ecotourism (Sillero-Zubiri & Laurenson, 2001). Indeed, most large carnivores can bring disproportionately large economic benefits through ecotourism compared to many other species; Sillero-Zubiri & Laurenson (2001) suggested that one leopard could bring US$50,000 in tourism revenue per year to Londolozi Game Reserve in South Africa. Furthermore, despite its potential to cause declines in carnivore abundance, sport and trophy hunting of carnivores is hugely important for the economy of many developing countries (Baker, 1997). Indeed, it can increase the financial productivity of areas of land considered unsuitable or unpopular for eco-tourism (Lindsey *et al*., 2007; Rosenblatt *et al.*, 2014).

Ecological importance

Carnivores are fundamental to ecological functioning as they control ecosystems from the top down (Treves & Karanth, 2003). By creating "landscapes of fear", they influence the abundance and distribution of prey species, which prevents over-grazing and the subsequent loss of habitat for many bird and insect species (Treves & Karanth, 2003; Ripple *et al*., 2014). By preventing an overabundance of herbivores, carnivores can indirectly contribute to the correct functioning of rivers and nutrient cycles in an ecosystem (Ripple & Beschta, 2004; Fortin *et al.,* 2005; Steneck, 2005). However, when human-carnivore conflict leads to the loss of carnivores from an ecosystem, a series of linked negative events - known as a trophic cascade - occurs (Ripple *et al*., 2014). To ensure that ecosystems remain in their most productive and functional state, it is essential to maintain viable carnivore populations (Ripple *et al*., 2014). In cases where carnivores have been completely extirpated from ecosystems, reintroductions are an important conservation management tool (IUCN/SSC, 2013; Ripple *et al*., 2014).

1.3 Reintroduction Biology

Situated in the wider field of restoration ecology, carnivore reintroductions are part of an historically preservationist field of "conservation translocations" which can be divided in to "reinforcements" and "reintroductions" (IUCN/SSC, 2013; Corlett, 2016). Reinforcements are proactive, preventative measures which can increase the resilience of a population by adding unrelated individuals (IUCN/SSC, 2013; IUCN/SSC, n.d.). Reintroductions are more reactive and can be defined as "the

intentional release of an organism inside its indigenous range from which it has disappeared" (IUCN/SSC, 2013). Reintroductions aim to re-establish viable populations of species, however, much like human-carnivore conflict, reintroductions are not just a biological matter (IUCN/SSC, 2013). Reintroductions require an interdisciplinary perspective throughout planning, implementation and monitoring. Indeed, socio-economic and political factors are often far more important than biological factors in dictating the outcome of a reintroduction attempt (Sarrazin & Barbault, 1996; Treves & Karanth, 2003; IUCN/SSC, 2013).

1.3.1 Carnivore reintroductions

Carnivores are reintroduced to areas in which they were previously extant to ensure that top-down control of ecosystems can be re-established (Corlett, 2016). Often known as "trophic re-wilding" (Corlett, 2016; Svenning *et al.,* 2016), these introductions lead to positive trophic cascades whereby increased predation on herbivores reduces over grazing and promotes primary production (Fortin *et al*., 2005). A standout example of this occurred with the reintroduction of grey wolves (*Canis lupus*) to Yellowstone national park, USA (Fortin *et al*., 2005; Svenning *et al.,* 2016). This reintroduction, which began in 1995, created landscapes of fear and thus reduced the abundance and distribution of many herbivores, including elk (*Cervus canadensis*), which reduced grazing pressure in a number of locations (Ripple & Beschta, 2004). This reduction in grazing pressure created a trophic cascade whereby recruitment of tree species such as trembling aspen (*Populus tremuloides*) increased significantly (Fortin *et al*., 2005). This provided habitat for a number of bird and insect species and increased river functionality (Ripple & Beschta, 2012). The improvements in ecosystem functioning and the establishment of a self-sustaining wolf population allow us to consider this reintroduction a success. However, not all reintroduction attempts have been so successful.

A number of studies have attempted to review carnivore reintroductions (Beck *et al*., 1994; Wolf *et al.,* 1998; Breitenmoser *et al.*, 2001; Hayward *et al.,* 2007a). Breitenmoser *et al*. (2001) analysed 165 carnivore reintroductions which involved 22 species from five different families. They found that only 42% of these reintroductions could be considered successful. Furthermore, Hayward *et al.* (2007a), who focussed specifically on large carnivore reintroductions in Africa, found that only nine out of 30 reintroductions could be considered successful. Both Griffith *et al.* (1989) and Gusset *et al*. (2008) have suggested that translocations and reintroductions can be considered successful if they result in "self-sustaining population[s]". While this definition is logical, it is troublesome in its simplicity. How to define self-sustaining, over what time scale and at what population size are all questions which have concerned a number of authors (e.g., Hayward *et al*., 2007a; Jenkins *et al*., 2015). Gusset *et al.* (2008) focussed specifically on African wild dog reintroductions and proposed that if a pack were to survive and breed successfully in the landscape, they could be considered to be self-sustaining

and thus the reintroduction could be considered a success. It is clear that the requirements for success are unique for every reintroduction attempt, yet failures (which can be considered the death of reintroduced individuals) occur for a number of reasons (Gusset, 2009; Lewis *et al.,* 2012).

Inappropriate release site selection is an important reason for carnivore reintroduction failure (Breitenmoser *et al*., 2001; Armstrong & Seddon, 2007). When the habitat, climate and size of the release site are inappropriate for the species then the risk of failure is high (Seddon *et al*., 2007). A lack of knowledge concerning the genetic status of the released individuals can also be classified as a failure if it results in severe founder effects and inbreeding (Sarrazin & Barbault, 1996; IUCN/SSC, 2013). However, one of the greatest reasons for the failure of carnivore reintroduction projects is a lack of removal or management of the previous causes of carnivore extinction, most commonly human-carnivore conflict (Mills *et al.,* 1998; Breitenmoser *et al*., 2001; Gusset *et al.,* 2008; Silva-Opps & Opps, 2011; IUCN/SSC, 2013). If this is not resolved, and the socio-economic and political problems of communities surrounding carnivore release sites are not improved or worsen, then reintroductions will most likely fail (Mills *et al.,* 1998; Gusset *et al.,* 2008; IUCN/SSC, 2013). Indeed, it is important to ensure that the reintroduction of a carnivore does not generate new human-carnivore conflict and as a consequence result in their retributive killing by local communities (Van Wieren, 2012; Fraser-Celin *et al.,* 2017).

The life history of many carnivore species means that they are far ranging and elusive and thus it is difficult and extremely expensive to monitor individuals following their release. This explains in part the lack of post-release monitoring which in turn has clouded an assessment of the success or failure of many carnivore reintroductions (Hayward *et al*., 2007a; Gusset, 2009; IUCN/SSC, 2013). Evidence-based conservation and adaptive management are becoming essential tools in efforts to conserve some of our most endangered species and they need to be prioritised when budgeting for reintroductions (Gusset *et al.,* 2008).

Reintroductions remain a controversial, yet increasingly important tool in carnivore conservation. They have helped to increase the abundance and distribution of declining carnivore species and restore the functioning of many ecosystems (IUCN/SSC, 2013). However, they are extremely expensive and limited by their single species focus (Seddon *et al*., 2005). Reintroductions are simply one tool in a set of conservation management techniques which ensure the persistence of carnivores in an increasingly inhospitable landscape (Ripple *et al*., 2014).

1.4 Metapopulation Biology

A metapopulation can be defined as "a set of spatially discrete subpopulations that display asynchronous population dynamics, and where migration between one or more patches is possible" (Davies-Mostert *et al*., 2009). Metapopulations occur when habitat is fragmented and populations are not continuously distributed. While some metapopulations occur naturally, the majority of metapopulations today are a result of human-induced habitat fragmentation (Miller *et al*., 2015). Metapopulations require unique conservation management techniques due to the threats which small, fragmented populations face (Davies-Mostert *et al*., 2015). Efforts to control sex ratio, birth and death rates, genetic drift and environmental pressures all require greater attention than when managing large continuous populations (Davies-Mostert *et al*., 2015). However, the spatial separation of metapopulations can be beneficial when attempting to manage disease transmission and environmental stochasticity (Davies-Mostert *et al*., 2015).

1.4.1 Carnivore metapopulations

Historically, most carnivores had large and continuous ranges, however habitat fragmentation has led to the development of a number of carnivore metapopulations (Hanski & Gilpin, 1991; Gusset, 2009). An understanding of single species metapopulation dynamics is thus essential for the future management of many carnivore species including lion, cheetah (*Acinonyx jubatus*) and African wild dog. The development of human-induced metapopulations requires a new set of management techniques which can potentially include the simulation of emigration and immigration via "human-mediated movement" (Akçakaya *et al*., 2006). Such management can be crucial in maintaining the presence of carnivores in ecosystems. However, when carnivores have been completely extirpated from landscapes and no vast areas of land are available for a single reintroduction, it is possible to establish a metapopulation through a series of reintroductions of smaller, geographically separated populations (Davies-Mostert *et al*., 2015).

1.4.2 Managed metapopulations

As a species which once ranged throughout Africa, the African wild dog has suffered significant range contractions due to human-carnivore conflict, habitat fragmentation and prey decline (Silva-Opps & Opps, 2011; Jenkins *et al*., 2015). It is now considered to be the most endangered large carnivore in southern Africa and has a total population of around 6000 individuals (Davies-Mostert *et al*., 2009; IUCN, 2012; Jenkins *et al*., 2015; Fraser-Celin *et al.,* 2017). After significant population declines in the late 1990s which reduced the total number of viable populations in South Africa to one (in Kruger National Park), a meeting was held to discuss the future of the species and the decision was taken to try to establish a second viable population in South Africa (Mills *et al.*, 1998; Gusset,

2009; Davies-Mostert *et al*., 2015). Due to the wide-ranging nature of African wild dogs, there was no single piece of land available to establish this second population and thus a "managed metapopulation approach" (MMA) in smaller fenced reserves was adopted (Davies-Mostert *et al*., 2015).

The introduction of multiple packs of African wild dogs to reserves throughout South Africa enabled the development of nine new packs, comprising 202 individuals (Davies-Mostert *et al*., 2015). The introduced packs were managed as a single population and by transporting individuals between each reserve natural emigration and immigration were simulated (Davies-Mostert *et al*., 2009). The MMA provided the opportunity to collect data on key life history traits such as reproduction and survival as well as movement patterns within each reintroduction site (Jenkins *et al.,* 2015; Whittington-Jones *et al*., 2014). As there was no predictive framework to identify those conservation techniques which led to the greatest successes in African wild dog reintroductions, the importance of monitoring and evaluation post release was emphasised in order to both improve the knowledge base surrounding this species and inform future reintroductions (Gusset *et al.,* 2008). The MMA was undeniably logistically complicated and both time and cost intensive. However, for a species such as the African wild dog, which now only occurs in 10% of its original geographic range, this approach was certainly beneficial to reducing the probability of extinction from stochastic events (Ripple *et al.,* 2014). This MMA has been so successful that African wild dogs are now being introduced to countries neighbouring South Africa including Botswana and Mozambique.

1.5 Animal Movement Ecology

The movement behaviour of most carnivore species is based on ecological, environmental and social requirements (Davies-Mostert *et al*., 2015). Carnivores move in order to ensure that they have sufficient food resources, a reduced predation threat and increased mating possibilities (Davies-Mostert *et al*., 2015). Movement is a response to heterogeneity within a landscape and has a key influence on biodiversity and ecological interactions at all levels of an ecosystem (Nathan *et al*., 2008; Van Moorter *et al.,* 2009; Jeltsch *et al.,* 2013). Relatively recent advances in GPS technology has allowed the development of a Lagrangian approach to animal movement analysis (Nathan *et al*., 2008). Developed from a Eulerian approach to monitoring overall population movement and distribution, the Lagrangian approach allows the identification of an individuals' movement pathway through time and space (Nathan *et al*., 2008). Nathan *et al*. (2008) suggested that movement was the response to the internal state, motion ability and navigation capacity of an individual. The internal state encompasses the individual's knowledge and reasoning for movement; the motion ability defines how the individual moves and the navigation capacity determines the timing and direction of movement which are driven by abiotic and biotic factors and are based on goal achievement (Nathan *et al*., 2008; Valeix *et al.*, 2010). For example, there may be a goal to move from one location to

another to avoid predation or reach a prey source. Movement, driven by a navigation capacity, is the mechanism by which this goal can be achieved. Navigation capacity is one of the most complex and burgeoning fields of movement ecology; it is a crucial aspect of human-carnivore conflict which must be managed to bring about conflict mitigation strategies (Nathan *et al*., 2008).

Movement between patches is a key feature of a metapopulation (Jeltsch *et al.,* 2013). Jeltsch *et al.* (2013) proposed the idea of "mobile links" as the individuals which move to connect sub-populations. These authors further subdivided mobile links in to resource linkers, genetic linkers and process linkers. While all three are crucial in metapopulation biology, process linkers are perhaps the most important in carnivore metapopulation movement ecology. Process linkers are crucial for wider ecosystem functioning, as they perform roles such as predation (Jeltsch *et al.,* 2013). In managed metapopulations, humans become the mobile links, as only with direct and intense human inputs can managed metapopulations have functional mobility (Akçakaya *et al*., 2006). A managed metapopulation approach can provide a rare opportunity to collect data and perform meta-analyses concerning the movement ecology of individuals and the way in which metapopulations function (Davies-Mostert *et al*., 2015).

Movement ecology and meta-analysis can provide incredibly useful tools for determining the success of a reintroduction attempt (Berger-Tal & Saltz, 2014). By exploring their surroundings, reintroduced individuals identify the best sites for resource exploitation (Berger-Tal & Saltz, 2014). Known as the "exploration-exploitation trade-off" (Berger-Tal & Saltz, 2014) reintroduced animals must strike a balance between learning about their new environment through costly exploration or preserving energy through exploiting familiar resources (Berger-Tal & Saltz, 2014). Berger-Tal & Saltz (2014) suggested that a reintroduction could be considered a success when "post-release behavioural modification" from exploration to exploitation is observed. This transition demonstrates knowledge development and thus a change in the "internal state" driver of movement (Nathan *et al*., 2008). By transitioning to exploitative habits, we can infer that site fidelity has developed and a home range has been established (Powell, 2000).

1.6 Meta-analysis

1.6.1 Home range

A home range encompasses the "areas about [the animal's] established home which is traversed by the animal in its normal activities of food gathering, mating and caring for young" (Burt, 1943). Almost all species have home ranges. Powell and Mitchell (2012) and Spencer (2012) suggested that this was the result of the use of memory to create a "cognitive map" of the most preferred areas in a landscape. While most species have home ranges, they vary massively in size. Gittleman and Harvey

(1982) proposed that "metabolic needs" determined the size of home ranges; those species requiring more meat in their diet generally had larger home ranges. Pomilia *et al.* (2015) acknowledged that food abundance was an important factor determining the size and location of home ranges for African wild dogs in northern Botswana, however, they also recognised the influence of abiotic climatic factors such as temperature and precipitation on home range development. The majority of home ranges have core areas in which individuals focus their activities (Powell, 2000). The location of den sites or high prey density will most likely influence the location of these core areas (Silva-Opps and Opps, 2011).

In the case of reintroduced carnivores, a home range is established once sufficient investigations have taken place (Spencer, 2012). However, the importance of understanding home ranges was highlighted in the case of African wild dogs reintroduced to Kwa-Zulu Natal in South Africa. Silva-Opps & Opps (2011) and Jenkins *et al*. (2015) both found that packs of African wild dogs had home ranges larger than the reserves into which they had been introduced. Such a finding highlights the importance of including land surrounding protected areas in conservation planning (Fraser-Celin *et al.,* 2017). Through investigating home ranges, we can begin to understand how barriers in landscapes affect the movements of individuals.

1.6.2 Habitat resistance

Barriers are intended to control the movement and dispersal ability of select species. Barriers such as rivers and mountain ranges are natural features in landscapes while metal fences are one of many human-derived barriers that can significantly restrict the ranging behaviour of many carnivore species (Blanco *et al.*, 2005; Cozzi *et al.,* 2013). Such restrictions on carnivore movement can release ungulate species from predation pressure, thus having a significant impact on ecological structure and multi-species movement ecology (Cozzi *et al.,* 2013).

Blanco *et al.* (2005) showed that fences were permeable to wolves in northern Spain, however rivers significantly limited their movement. Cozzi *et al.* (2013) supported this finding by showing that artificial fences were impermeable to lions yet permeable to a number of smaller carnivores including cheetah and African wild dog in northern Botswana. These authors also showed that rivers were permeable to lions but almost completely impermeable to African wild dogs (Cozzi *et al.,* 2013). The IUCN (2012) has highlighted the need to understand the impact of landscape features on the movement of African wild dogs. By understanding how this species interacts with barriers we can attempt to highlight areas in which African wild dogs may come in to contact with livestock and thus more carefully map areas of potential human-wild dog conflict.

1.6.3 Resource utilisation

Individuals use habitats and terrains (resources) to increase their fitness (Kertson & Marzluff, 2010; Silva-Opps & Opps, 2011). Whether in an attempt to avoid predation or increase access to food resources, this selection takes place progressively as the cognitive map of a landscape is increased (Silva-Opps and Opps, 2011). Many authors have suggested that African wild dog resource selection and use in Botswana and South Africa is a response to predation and kleptoparasitism (van Dyk & Slotow, 2003; Jackson *et al*., 2014; Whittington-Jones *et al*., 2014; Jenkins *et al.,* 2015). Lions and spotted hyena (*Crocuta crocuta*) are believed to be responsible for around 30% and 6% of all wild dog pup mortality respectively (Mills & Gorman, 1997; Jackson *et al*., 2014). Thus, African wild dogs select resources which allow them to increase hunting success whilst avoiding threats from larger carnivores. Whittington-Jones *et al*. (2014) and Jenkins *et al*. (2015) found that packs of African wild dogs select habitats of thicket woodland in rough and rocky terrains. The selection of these types of resources is considered to be an active avoidance of flat-lying, open and prey dense areas which are often dominated by interspecific competitors such as lions (van Dyk & Slotow, 2003; Jackson *et al*., 2014, Snyman, 2016). Thus, resource selection and utilisation can be considered as "defence mechanism[s]" (Jackson *et al*., 2014).

Resource selection and utilisation are particularly important considerations in carnivore reintroduction planning. In the case of African wild dog reintroductions, it is important to consider the heterogeneity of resources at the release site and the availability of "competition refuges" (Jackson *et al*., 2014) whereby packs can avoid predation by lions and kleptoparasitism by spotted hyenas.

1.7 Study Rationale

In order to prevent further declines in African wild dog populations, a network of reintroductions was developed throughout South Africa and an MMA was adopted (Davies-Mostert *et al*., 2015). Between 1998 and 2006, a total of nine reintroductions took place which added around 200 individuals to the country's African wild dog population (Davies-Mostert *et al*., 2015). Despite many successes, reintroductions remain a costly conservation exercise which, when high failure rates are factored in, threatens the long-term viability of this management technique (Hayward *et al*., 2007b). There have been many attempts to evaluate individual reintroductions which highlight the importance of learning from every reintroduction (van Dyk & Slotow, 2003; Whittington-Jones *et al*., 2014; Jenkins *et al*., 2015; Potgieter *et al.*, 2015). By increasing our knowledge of how African wild dogs interact with new landscapes we can inform and improve future reintroduction attempts. The purpose of this study is to conduct an assessment of the way in which an introduced pack of African wild dogs (subsequently referred to as 'wild dogs') utilised the landscape in and around the Northern Tuli Game Reserve (NTGR) in eastern Botswana.

1.7.1 Objectives

The objectives of this study include determining:

1) How the home range of the introduced pack changed on a monthly basis.
2) How artificial and natural barriers within the landscape impacted the movements of the introduced pack.
3) Which terrains and landscape types the introduced pack used.

1.7.2 Predictions

Similar to the findings of Pomilia *et al.* (2015) I predict that the home range of this pack will remain consistently large in size and if the home range contracts significantly, I would consider this as possible evidence of a transition from exploration to exploitation-based activities in the landscape (Pomilia *et al*., 2015). Based on the size of the NTGR and the lack of conspecific competition, I predict that the time length of this study will not be sufficient to see a complete transition from explorative to exploitative activities as I predict that this complete transition will take close to a year to occur (Berger-Tal & Saltz, 2014). I predict that artificial barriers (such as game and veterinary cordon fences) will impede the movements of the pack, however I believe that natural barriers such as flowing rivers will have the most significant impact on the movements of this pack (Cozzi *et al*., 2013). Finally, following the work of Jackson *et al.* (2014), Whittington-Jones *et al*. (2014) and Jenkins *et al.* (2015), I predict that the introduced pack will select rough and rocky terrains, while avoiding low-lying elevations and riverine areas (Mills & Gorman, 1997; Gusset *et al.,* 2008; Jackson *et al*., 2014).

2. METHODS

2.1 Study Site

Located between 21°55' and 22°15'S and 28°55' and 29°15'E in the eastern corner of Botswana, the Northern Tuli Game Reserve (NTGR) spans 72,000ha (720 km^2) and forms part of the Tuli Block and the Greater Mapungubwe Transfrontier Conservation Area (GMTCA) (Notugre, 2017) (Figure 1). Bordering the Mapungubwe National Park to the south in South Africa and the Tuli Hunting Safari Block (THSB) (often referred to as the Tuli Circle) to the north-east in Zimbabwe, the NTGR is located in the summer rainfall region of southern Africa; this area receives the majority of its rainfall between October and March in the form of large thunderstorms and rain showers (Darkey & Alexander, 2014; Notugre, 2017). Between April and September, the region is dominated by the Kalahari high-pressure system which brings cool and dry winters. The temperature in this region ranges between -5°C and 42°C (Notugre, 2017).

The NTGR falls within the hardveld region of Botswana and contains a wide variety of habitat and terrain types including savanna, riverine forests, open plains and sandstone cliffs (Mashatu, 2017; Notugre, 2017). Whilst the hardveld is known to be one of the most agriculturally productive regions of Botswana, the majority of soils in the NTGR are shallow and of poor quality (Notugre, 2017). The rich, fertile soils are constrained to the riverine areas of the NTGR (Notugre, 2017). Two main rivers dominate the NTGR, the Limpopo and the Shashe, which form the southern and north-eastern boundaries of the NTGR respectively (Notugre, 2017). The Limpopo is a large, perennial river whereas the Shashe is a smaller, ephemeral river, commonly dry during the winter months. The western boundary of NTGR is defined by an electrified game fence (Jackson *et al*., 2012). This fence (hereafter referred to as the Northern Tuli Game Reserve (NTGR) fence) is 2.1m high and has electrified strands at 1.8m, 50cm and 20cm from the ground - it is frequently damaged by elephants (*Loxodonta africana*) and is poorly maintained (Brassine, 2014). There is an additional veterinary cordon fence (hereafter referred to the as the foot and mouth (FM) fence) in the south-west of NTGR which was erected to prevent the spread of foot and mouth disease. However, this fence is also damaged and is readily traversed by most animals (Brassine, 2014).

Botswana has around 700-800 wild dogs, the majority of packs are found in the north-western parts of the country, however multiple packs have been recorded ranging far in to the south and south-east of Botswana (Woodroffe *et al*., 2004; IUCN/SSC, 2015). One pack of 18 wild dogs was introduced to NTGR in early 2008 (Jackson *et al*., 2012). A combination of pack dispersal, snaring and poisoning events contributed to the demise of this pack by 2011, but movement data collected did suggest bio-boundaries might influence the movements of future introduced packs (Jackson *et al.,* 2012; Synman

A., Pers comm. 2017). Wild dogs have not been resident in the NTGR since 2012, however random sightings of single individuals have been noted in the south-west (Brassine, 2014). In the far south-west of the Tuli Block, a fenced reserve named 'Limpopo Lipadi' holds one resident pack (Limpopo Lipadi, 2017).

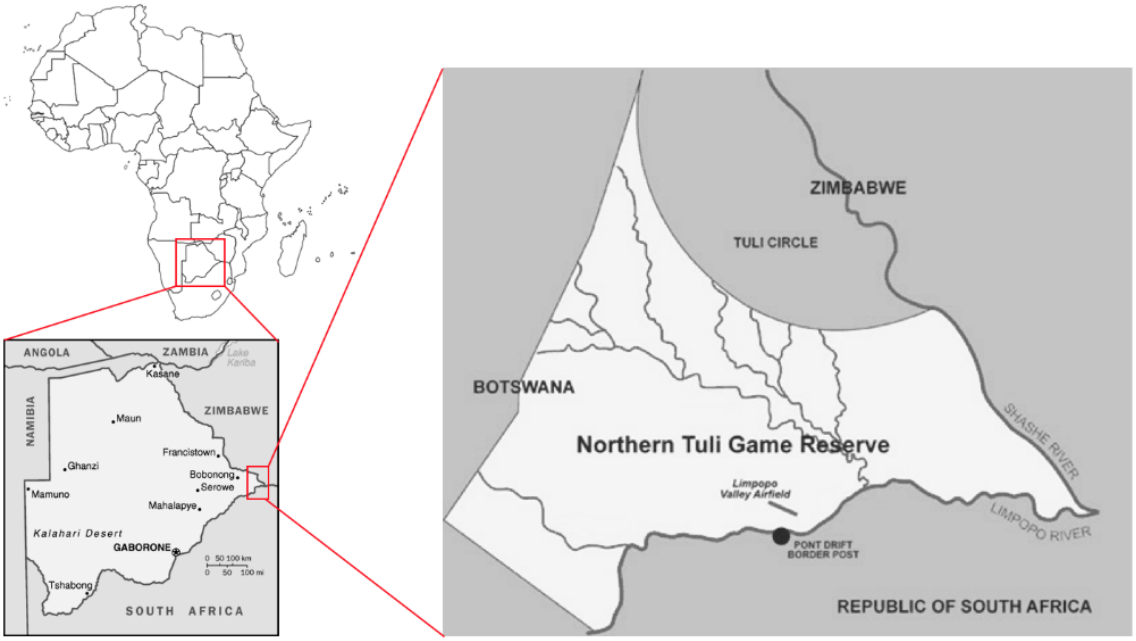


Figure 1: Location of the Northern Tuli Game Reserve (NTGR) in south-eastern Botswana into which a pack of eight African wild dogs were introduced in December 2016.

2.2 Study Animals

A group of eight wild dogs was transported to the NTGR on 13th December 2016. The pack, which comprised three adult males and five adult females, originated from Tembe Elephant Park (TEP) in Kwa-Zulu Natal, South Africa. The individuals introduced to the NTGR formed part of an excess population which TEP did not have the capacity to accommodate (Snyman A., Pers comm. 2017). Thus, whilst this pack is part of the larger wild dog metapopulation, their reintroduction was not specifically planned by the Wild Dog Advisory Group of South Africa (WAG-SA, 2017).

The pack was initially placed in a boma (13th December 2016 to 16th February 2017) with the sexes separated by an internal fence, but after four days the males managed to break through the internal fence and joined the females (Snyman A., Pers comm. 2017). Two GPS satellite collars (Africa Wildlife Tracking, Pretoria, South Africa) were deployed on one male and one female in the group believed to be the alpha pair (Snyman A., Pers comm. 2017). Approval for this work was provided by Botswana's Ministry of Environment, Wildlife and Tourism (Reference: EWT 8/36/4 XXXIII (48) (Appendix 1)).

When studying group living animals it is usually sufficient to place a GPS collar on only one animal which serves as proxy for the whole groups' movement (Silva-Opps & Opps, 2011; Hoffman and O'Riain, 2012). However, when the option arises to use more than one collar it is beneficial to do so in case one collar malfunctions or the collared individual dies. Additionally, collaring an individual from each sex ensures that movements can still be recorded even in situations where a pack splits into different sex groups (Snyman A., Pers comm. 2017). The collar fitted to the male wild dog stopped recording GPS locations on 15th July 2017. Due to the discovery of the individual's collar at the entrance to a spotted hyena (*Crocuta crocuta*) den this individual is believed to have died (Snyman A., Pers comm. 2017). The female's collar continued to provide data which were used for all subsequent analyses. This collar has been recording four GPS locations per day (8 am, 5 pm, 7 pm and 8 pm Central Africa Time - CAT) in addition to altitude and temperature. The male's GPS collar was set to record locations in the morning and early afternoon, the female's collar was set to record locations in the early morning and late afternoon. Thus, by utilising data from only the female's collar, the majority of GPS locations used in this study represent afternoon movements.

2.3 Data Analyses

2.3.1 Home range

I calculated utilisation distributions (UDs) to show minimum convex polygons (MCPs) and kernel density estimations (KDEs) to provide the probability of a particular animal being found in a particular location (Powell, 2000; Jenkins *et al.*, 2015). 100% MCPs were initially constructed to visualise the largest area in which the wild dogs were active. Thereafter, by using the UDs, 50% and 95% isopleths were created to demarcate the core areas and outer boundaries of the home range respectively (Jenkins *et al*., 2015). Plugin bandwidth was chosen for its detailed qualities. Whilst spatio-temporal autocorrelation is a concern in home range analysis; all data points were included to provide detailed information on how the pack moved through the landscape (Pomilia *et al*., 2015; Welch *et al.,* 2015). Using the package 'Reproducible Home Range (RHR)' in R (v 1.1.383, R Core Team, 2016), MCPs and KDEs were constructed for each 'month' since release. 'Months' were set as 28-day periods starting from the 16th February 2017 and ending on the 25th October 2017, to produce a final data set of nine months.

Utilisation distribution overlap index (UDOI) analysis using the 95% UD results was conducted in R (v 1.1.383, R Core Team, 2016). This was used to understand the intensity of area use within the general home range by providing an estimate of the proportional overlap between consecutive months. Centre-point analysis was used to identify the GPS location of the centre of each month's home range using ArcGIS version 10.4 (ESRI, 2016). These analyses were used to identify whether movement patterns were becoming more predictable with time and whether a stable home range was

emerging (i.e. the centre points of monthly home ranges were spatially closer). Daily distance moved was used to identify how the pack was moving within the landscape. This analysis was conducted using Home Range Tools in ArcGIS version 10.4 (ESRI, 2016).

2.3.2 Habitat resistance

The study site is bounded on two sides by metal fencing and on the other two sides by rivers, all four of these 'barriers' were used in the habitat resistance analysis. The metal fences comprise the NTGR fence and the FM fence (Figure 3). The NTGR fence runs from north-east to south-west, with the north-easterly section denoting the main western boundary of the NTGR. The FM fence marks the south-western boundary of the NTGR and runs from north-west to south-east. The rivers bounding the study site are the Limpopo and Shashe rivers (Figure 3). The north bank of the Limpopo marks the southern boundary of the NTGR as well as the border between South Africa and Botswana. The Shashe river runs from north-west to south-east through Zimbabwe and Botswana. The west bank marks the eastern boundary of the NTGR in Botswana, it also marks the eastern boundary of the THSB in Zimbabwe and the border between Botswana and Zimbabwe (Figure 3). Habitat resistance was analysed using all GPS locations recorded within 10km of all four barriers.

Barrier effect

Barriers were considered to affect the movements of the wild dogs if there was a significant ($p < 0.05$) difference in the number of GPS locations on either side of the barrier (Cozzi *et al*., 2013). Some studies have suggested that in order to avoid spatio-temporal autocorrelation only one GPS locations should be used per day i.e. detection data (Zeller *et al*., 2012). In this study, I chose to include all data points and adopt a pathway data approach to understand how the movement of individuals (rather than just their location) was impacted by barriers (Zeller *et al*., 2012). Initially, all GPS locations within 3-5 km of the barrier were put into 1 km wide bins, those points within 0-3 km of the barrier were put into 0.5 km wide bins to provide a greater level of detail. By binning the data, I was able to investigate the effect of distance from the barrier on pack movement. The total number of GPS locations in each bin on either side of the barrier was counted. A chi-squared goodness of fit test was used to show significant ($p < 0.05$) differences between the observed total of GPS locations in corresponding bins on either side of the barriers and the expected even distribution of points in corresponding bins. If there was no significant difference then I inferred that the barrier did not have an impact on the movements of the wild dogs.

Crossing likelihood

This was initially assessed using pathway data to identify the number of times barriers were crossed and comparing this to the number of times barriers could have been crossed but were not (Cozzi *et al*.,

2013). Steps were created by linking consecutive GPS locations using Home Range Tools in ArcGIS version 10.4 (ESRI, 2016). A generalised linear model (GLM) with a binomial distribution was used to identify significant ($p < 0.05$) effects on crossing likelihood with crossing steps set as 1 and non-crossing steps set as 0. Steps (crossing vs non-crossing) were set as a binary response variable in the model. Distance from the barrier, total lagged monthly rainfall and a distance and rainfall interaction effect were set as fixed effects in the model (Cozzi *et al*., 2013). All analysis was conducted using R statistical software (v 1.1.383, R Core Team, 2016).

Total monthly rainfall data, lagged by a month, was used to infer river flow. This rainfall data was the only information available within the time frame of this study and was obtained from Mashatu main camp located within the NTGR (Snyman A., Pers comm. 2017). It is important to acknowledge that by using this data I am making an assumption that rainfall in this area is linked to river flow in other parts of the NTGR and the wider area. Given a longer study period I may have been able to use government records of river flow, however as these are only updated twice a year this information was not available during my study period. Thus, while it is important to acknowledge this assumption, it is my contention that rainfall data provides the only data that I could use as a possible proxy for the likelihood that there would be water in the rivers of the study area.

Barrier permeability

This was identified by using all steps within both 5 km and 1 km of the inside of the barriers (i.e. the side closest to the NTGR and THSB). Firstly, the average bearing of all the steps within 5km and 1km of all barriers was determined. Subsequently, all steps were divided in to four bearing categories; northerly (316-44^{o}), easterly (45-135^{o}), southerly (136-225^{o}) and westerly (226-315^{o}) and the category containing the most steps was used to identify the predominant movement vector of the pack around each barrier. A chi-squared goodness of fit test was used to identify any significant ($p < 0.05$) difference between the observed distribution of points between the four bearing categories and the expected even distribution of points between the four bearing categories. Those movements with a mean which was parallel to or perpendicular away from the barrier indicated barrier impermeability (Table 1). Those movements with a mean which was perpendicular towards the barrier indicated barrier permeability (Table 1) (Cozzi *et al*., 2013).

Table 1: Direction of movements around the Northern Tuli Game Reserve (NTGR) fence, the foot and mouth (FM) fence, the Shashe river and the Limpopo river required to indicate either barrier permeability or barrier impermeability for a pack of African wild dogs introduced to the Northern Tuli Game Reserve (NTGR). This pack will henceforth be referred to as 'the study pack'.

Barrier	Perpendicular movements	Parallel movements	Barrier permeability indication	Barrier impermeability indication
NTGR fence	East/West	North/South	West	North/East/South
FM fence	North/South	East/West	South	North/East/West
Shashe River	East/West	North/South	East	North/South/West
Limpopo River	North/South	East/West	South	North/East/West

2.3.3 Resource utilisation

Resource utilisation was identified using resource utilisation functions (RUFs) (Marzluff *et al*., 2004). As "continual probabilistic density functions" (Snyman, 2016), RUFs use utilisation distributions (UDs) to identify the level of resource use within a landscape and provide a comparison of resource use in one site relative to others (Snyman, 2016). All GPS locations were used in this analysis and I assumed that the whole landscape within the four barriers of the NTGR and THSB was available to the wild dogs. Multiple regression was used to identify correlations between UDs and resources (terrain/landscape features) (Marzluff *et al*., 2004). All results are based upon a change in utilisation as a result of a modelled increase in a particular resource (for example: increasing altitude). Thus, positive results indicate an increasing use and negative results indicate a decreasing use. Coefficients were standardised in order to compare the statistical significance of each resource (Snyman, 2016). The "Mater correlation function" was used to account for spatial autocorrelation (Snyman, 2016). All statistical analysis took place using the package ruf.fit in R (v 1.1.383, R Core Team, 2016).

Three variables were used in the resource utilisation analysis; distance from rivers, elevation and terrain ruggedness. Distance from rivers was calculated by identifying the distance from each GPS location to both rivers in the NTGR using the Euclidean distance tool in ArcGIS version 10.4 (ESRI, 2016). Both terrain ruggedness and elevation were calculated using a digital elevation model (DEM) at 30m spatial resolution (Jackson *et al*., 2014; Snyman, 2016). Elevation values were taken directly from this DEM. Terrain ruggedness was calculated using a terrain ruggedness index (TRI). Using the focal statistics spatial filler tool in ArcGIS version 10.4 (ESRI, 2016) a layer of grid cells was placed across the study site. By identifying the variation in the standard deviation of the elevation of a unit of 3x3m grid cells, the terrain ruggedness was identified (Snyman, 2016). An increased variation in the standard deviation indicates a rougher terrain whereas a reduced variation indicates a smoother terrain (Snyman, 2016). All statistical analysis took place using the package ruf.fit in R (v 1.1.383, R Core Team, 2016).

3. RESULTS

3.1 Home Range Area

A total of 933 GPS locations were recorded between 16th February 2017 and 25th October 2017. Using all of these data points, a 100% MCP analysis resulted in a home range estimation of 1937.13 km^2 (Figure 3), the 95% KDE home range area was 766.98 km^2 (Figure 4). The 50% KDE home range area was 140.61 km^2 (Figure 4).

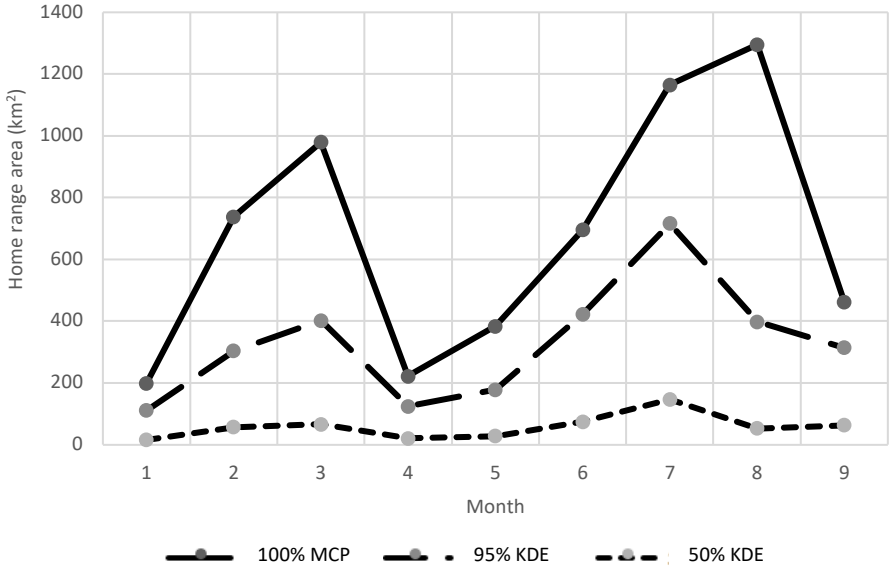


Figure 2: Monthly home range estimations for the study pack. The size of home range areas shown are 100% minimum convex polygon (MCP), 95% and 50% kernel density home range estimation (KDE) calculated with plugin bandwidth. Month 1 corresponds to the first month of GPS locations (Table 2).

The 933 locations were divided in to nine 28-day blocks to analyse the change in home range at a finer temporal scale. Ranging from 96 to 125, there was an average of 104 data points in each block (Table 2). 100% MCPs were calculated for these 28-day blocks, producing a range of areas from 198.68 km^2 (month 1) to 1295.49 km^2 (month 8) (Table 2; Figure 2). The mean monthly 100% MCP was 682.11± 377.71 km^2, the median monthly 100% MCP was 695.19 km^2. The 95% KDE results ranged from 110.82 km^2 (month 1) to 715.85 km^2 (month 7) and produced a mean monthly 95% home range area estimation of 330.02 ± 176.81 km^2, the median monthly 95% home range area estimation was 314.67 km^2 (Table 2; Figure 2). The 50% KDE results ranged from 15.89 km^2 (month 1) to 147.05 km^2 (month 7) and produced a mean monthly 50% core home range area estimation of 58.39 ± 37.13 km^2, the median monthly 50% KDE result was 56.84 km^2 (Table 2; Figure 2).

Table 2: Monthly home range estimations for the study pack. 100% minimum convex polygon (MCP) home range estimation, 95% and 50% kernel density home range estimations (KDE) calculated using plugin bandwidth.

Dates in 2017	Month	N of GPS locations	100% MCP (km^2)	95% KDE (km^2)	50% KDE (km^2)
16/02 – 15/03	1	125	198.68	110.82	15.89
16/03 – 12/04	2	103	738.21	303.36	56.84
13/04 – 10/05	3	101	979.21	401.88	66.17
11/05 - 07/06	4	107	222.05	125.03	20.77
08/06– 05/07	5	96	383.22	177.96	27.90
06/07 – 02/08	6	99	695.19	422.69	74.99
03/08 – 30/08	7	101	1164.89	715.85	147.05
31/08 – 27/09	8	100	1295.49	397.87	52.56
28/09 – 25/10	9	103	462.07	314.67	63.38

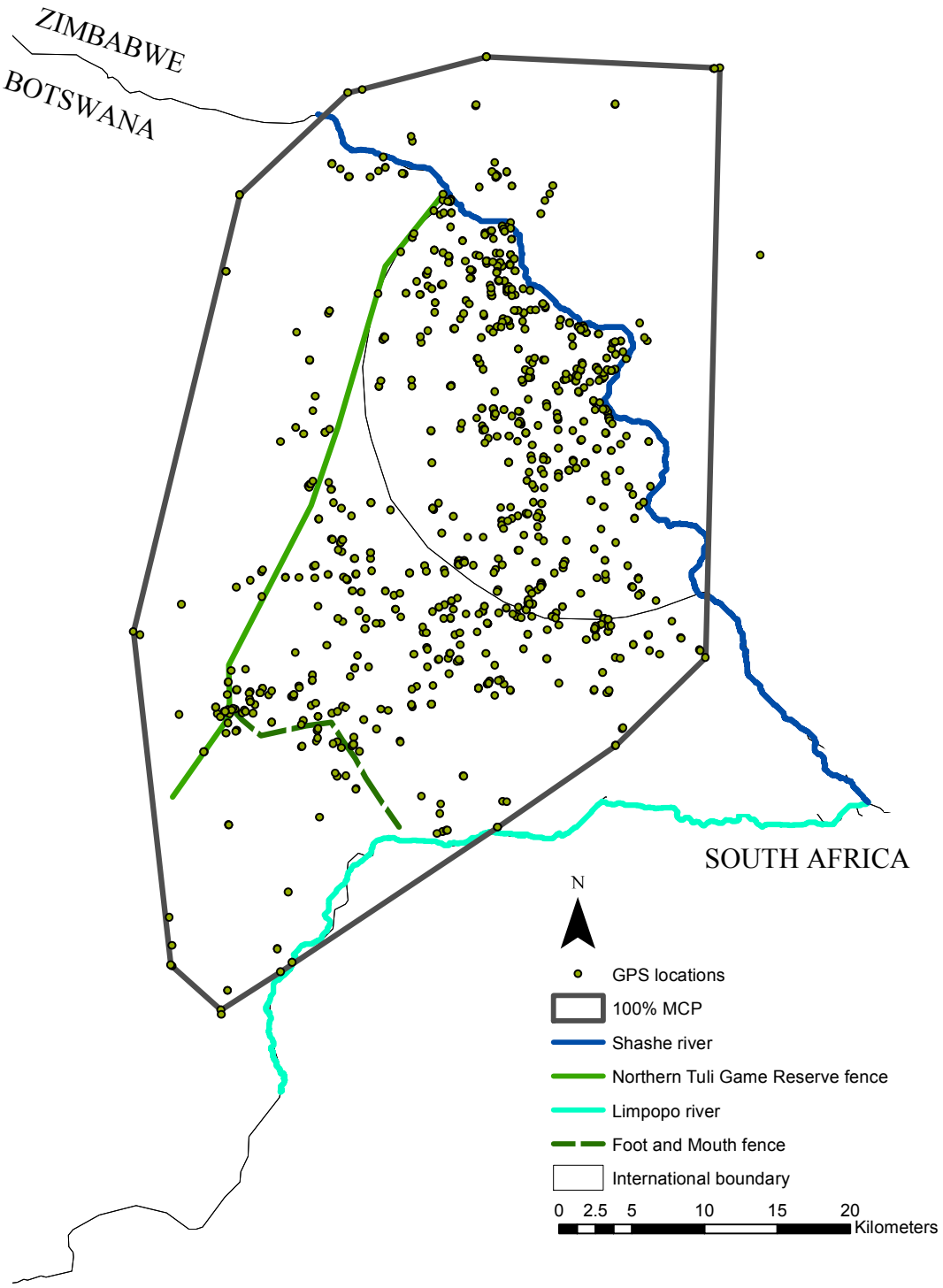


Figure 3: Map of the Northern Tuli Game Reserve (NTGR), showing all 933 locations recorded from a GPS collar placed on one member of the study pack. The solid polygon represents the overall 100% minimum convex polygon (MCP) estimation outline.

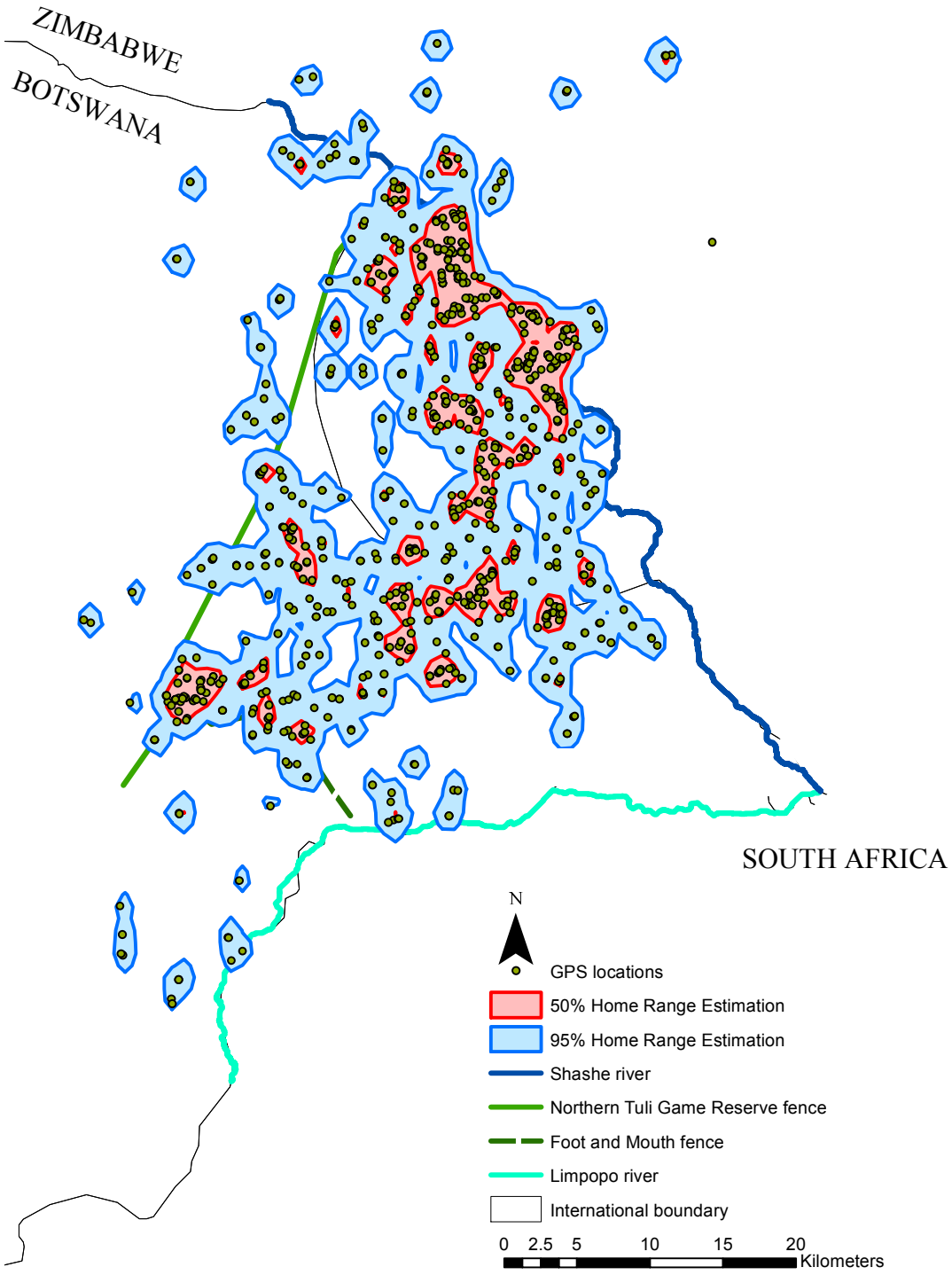


Figure 4: Map of the Northern Tuli Game Reserve (NTGR), showing all 933 locations recorded from a GPS collar placed on one member of the study pack. Both the overall 95% (blue) and the 50% (red) kernel density home range estimation (KDE) estimation outlines are shown.

3.1.1 Home range overlap

The UDOI results ranged from 0.00 (Month 4 and 1) to 1.08 (Month 2 and 8), with an average overlap of 0.51 (Figure 5; Appendix 2).

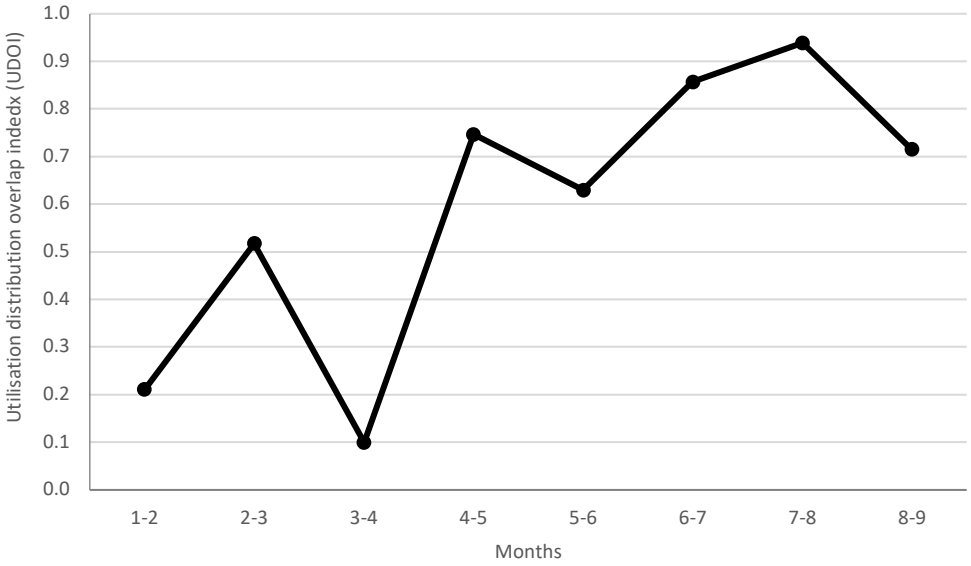


Figure 5: Utilisation distribution overlap index (UDOI) results for consecutive monthly 95% kernel density home range estimations (KDE) for the study pack.

Centre point analysis revealed that the maximum distance between the centre of each 95% KDE home range was 26.64 km (between month 3 and month 4). As shown in figure 6 the centre point of months 2, 6, 7, 8 and 9 were all concentrated within the south-west of the THSB.

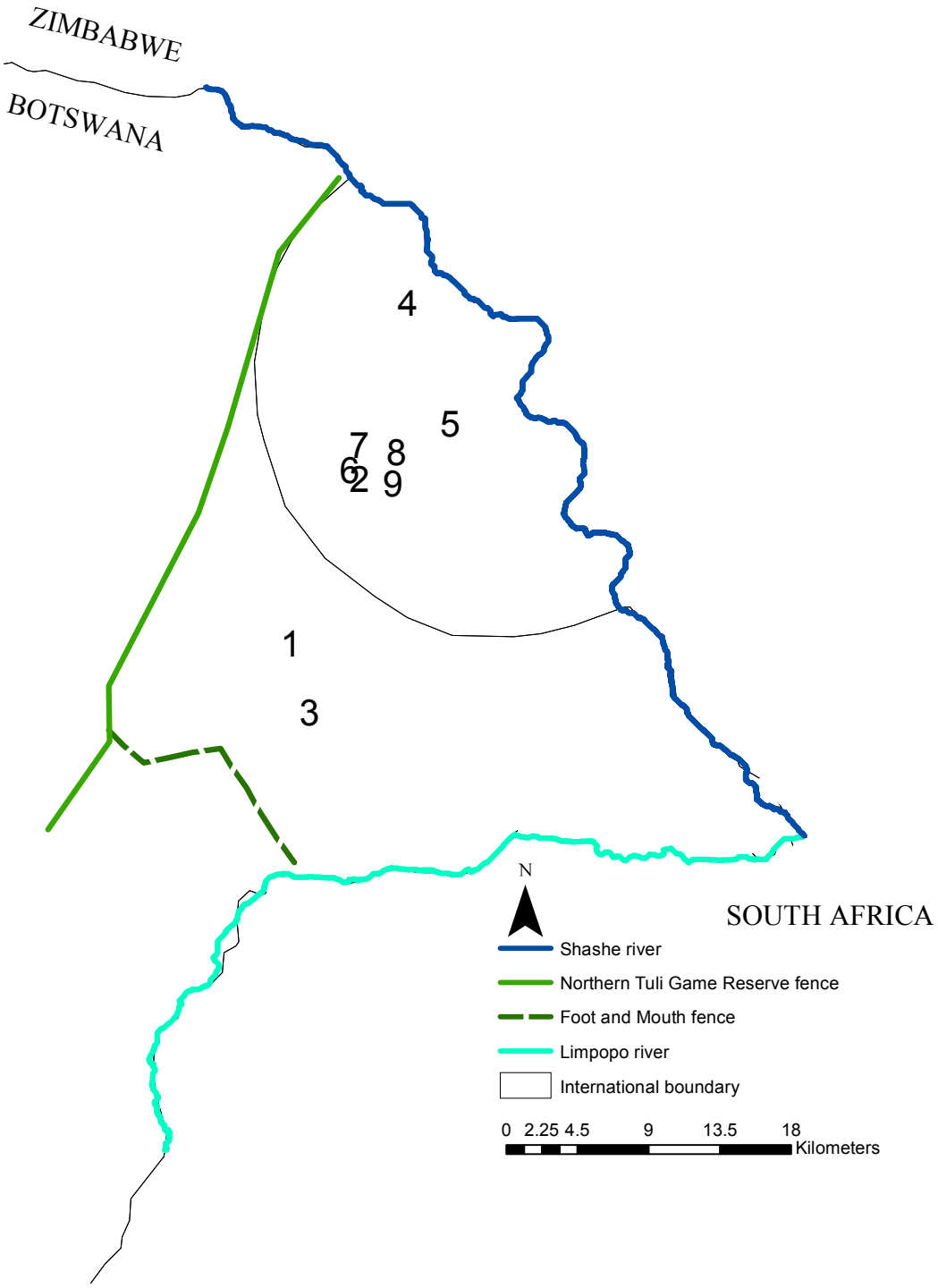


Figure 6: Map of the centre point of the monthly 95% kernel density home range estimation for the study pack.

3.1.2 Daily distance moved

Using all 933 data points, the daily distance moved was calculated on a monthly basis. The average daily distance moved in one month ranged from 4.44 km (month 1) to 12.04 km (month 7) (Figure 7; Appendix 3). The average daily distance moved for the nine-month study period was 8.37 km.

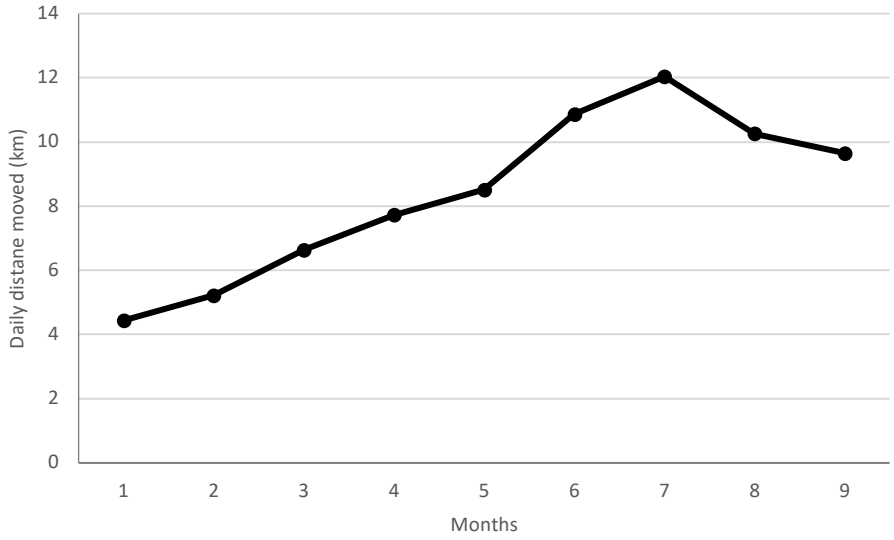


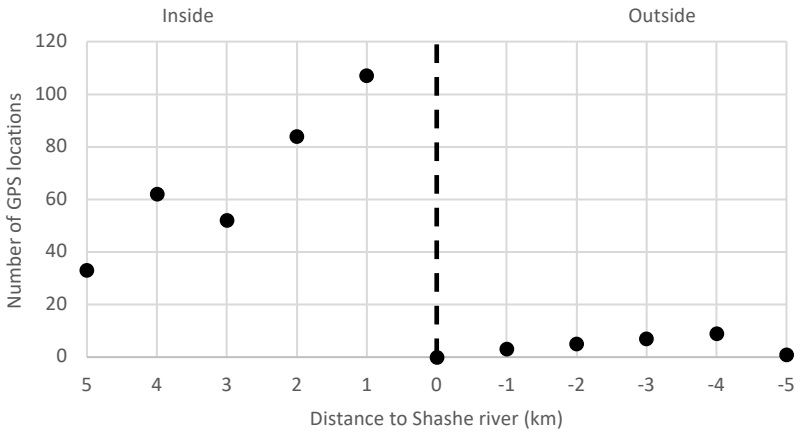
Figure 7: The average monthly daily distance moved by the study pack. Month 1 refers to the first 28 days of GPS locations (Table 2; Appendix 3).

3.2 Habitat Resistance

3.2.1 Barrier effect

Of a total of 932 steps recorded between February and October 2017, 64 included the crossing of a barrier. 24 of these steps included a river crossing and 40 included a fence crossing. There was a significant difference in the number of GPS locations on either side of the rivers, however this difference was less apparent on either side of the fences (Figure 8; Figure 9).

a)



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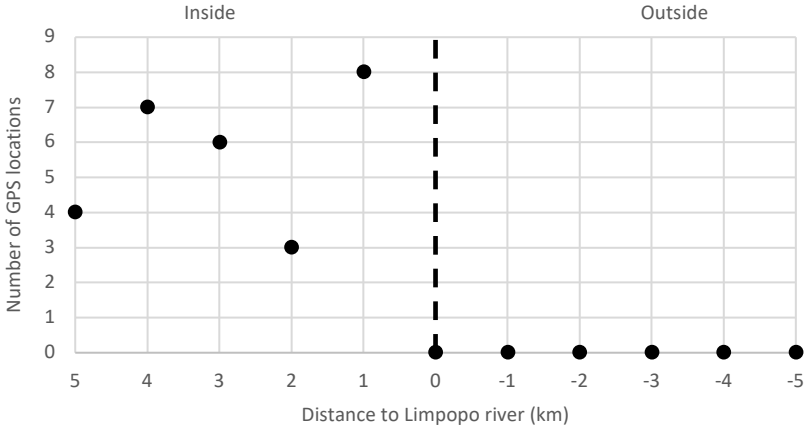
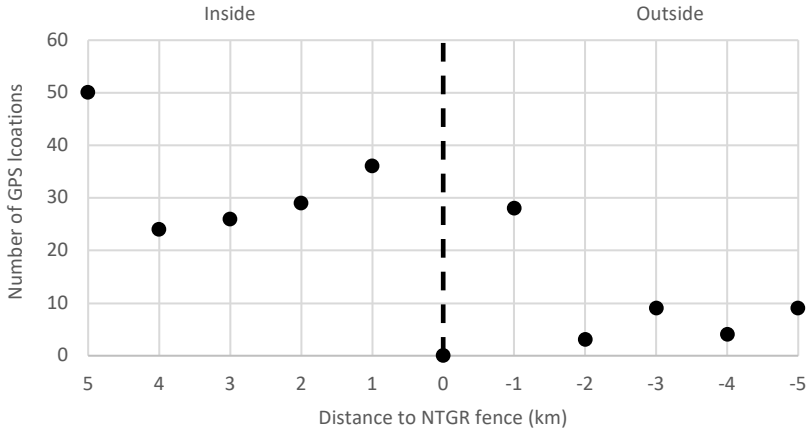


c)



d)

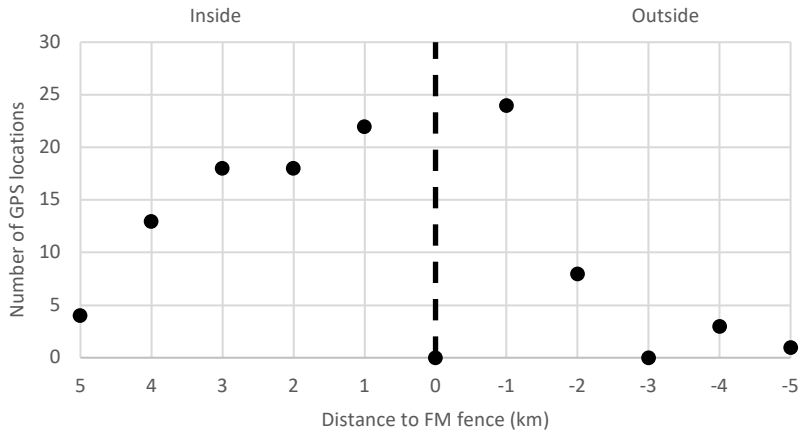


Figure 8: Total GPS locations recorded within 5km of landscape barriers for the study pack. The landscape barriers utilised are as follows: (a) the Shashe river, (b) the Limpopo river, (c) the Northern Tuli Game Reserve (NTGR) fence and (d) the Foot and Mouth (FM) fence.

Using a chi squared goodness of fit test a significant difference in the number of GPS locations on either side of the rivers within all distances from the physical barrier was identified. A significant difference was only observed in the points around the fences in the landscape when all points within 1.5 km (or greater) from the barrier were considered (Table 3).

Table 3: Chi-squared goodness of fit test results for the total GPS locations recorded for the study pack on either side of both rivers and fences in the Northern Tuli Game Reserve (NTGR) with a distance factor incorporated. Significant values ($p < 0.05$) indicated with *, degrees of freedom shown in brackets.

Distance from barrier (km)	Rivers p value	Rivers χ^2 value (df)	Fences p value	Fences χ^2 value (df)
0.5	3.2 e – 11*	44.08 (1)	0.68	0.164 (1)
1.0	<2.2 e – 16*	106.31 (1)	0.56	0.327 (1)
1.5	<2.2 e – 16*	157.37 (1)	0.0136 *	6.081 (1)
2.0	<2.2 e – 16*	179.22 (1)	0.001194*	10.50 (1)
2.5	<2.2 e – 16*	198.02 (1)	1.3 e – 05*	18.95 (1)
3.0	<2.2 e – 16*	218.27 (1)	2.22 e – 07*	26.83 (1)
4.0	<2.2 e – 16*	263.53 (1)	4.93 e – 11*	43.20 (1)
5.0	<2.2 e – 16*	297.39 (1)	< 2.2 e – 16*	69.30 (1)

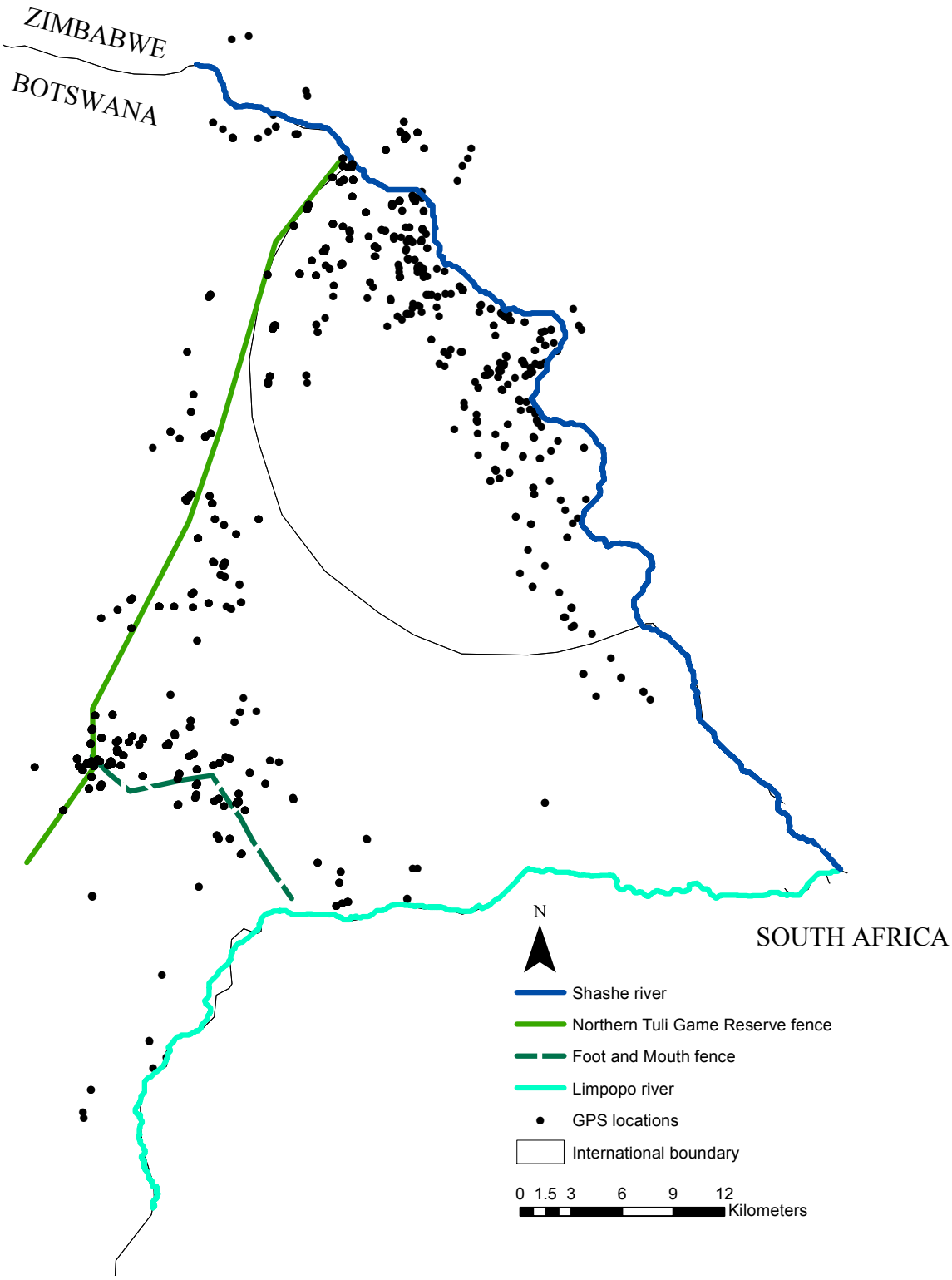


Figure 9: Map of the Northern Tuli Game Reserve (NTGR), with all GPS locations of the study pack recorded within 5 km of either side of the Shashe river, Limpopo river, Northern Tuli Game Reserve (NTGR) fence and Foot and Mouth (FM) fence.

3.2.2 Crossing likelihood

The average step length leading to a crossing event was 5.44 km in length. I therefore ran two GLMs for each barrier type with a binomial distribution to explore the likelihood of crossing a landscape barrier: one which included all GPS locations within 5 km of a barrier and one which included all GPS locations within 10 km of a barrier.

Fence-crossing likelihood

In both models, only distance from the fence was significant in determining fence crossing likelihood (Table 4).

Table 4: Results of a generalised linear model (GLM) analysis showing the influence of distance from fence and lagged monthly rainfall on the likelihood of the study pack crossing fences in the Northern Tuli Game Reserve (NTGR). Significance ($p < 0.05$) marked with *.

Distance from fence	Significant variables	P value	Beta estimate	Standard error
5 km	Distance from fence	0.00321*	-0.467707	0.158724
	Lagged monthly rainfall	0.65817	0.004296	0.00971
10 km	Distance from fence	3.74 e – 06*	0.002218	0.108726
	Lagged monthly rainfall	0.8119	-0.502882	0.00932

Due to the increased number of GPS locations utilised, only the results of the analysis which included all GPS locations within 10 km of the fences are shown below in figure 10.

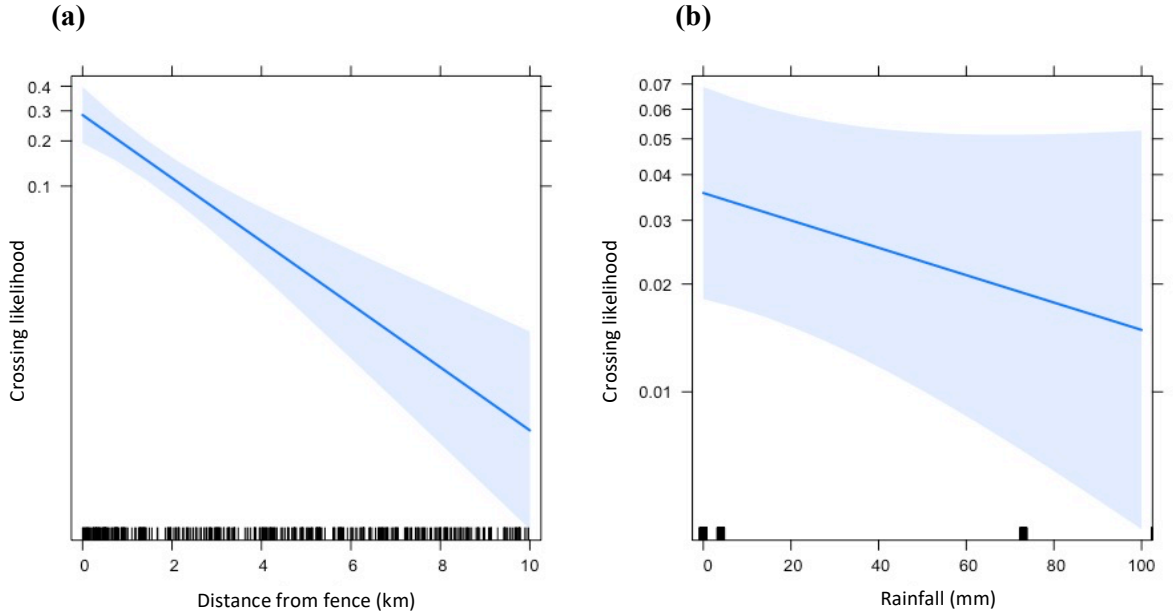


Figure 10: Likelihood of the study pack crossing a fence within the Northern Tuli Game Reserve (NTGR) as a result of (a) distance from the fence and (b) lagged total monthly rainfall when all GPS locations within 10 km of the fences are included.

River-crossing likelihood

The results from the GLM showed that both distance from the rivers and lagged monthly rainfall were significant variables in determining the river crossing likelihood when all GPS locations within 10km of the rivers were considered (Table 5). When all GPS locations within 5km of the rivers were considered, distance from the rivers was significant in determining river crossing likelihood, lagged monthly rainfall was slightly less significant (p = 0.06) than the other variables (Table 5).

Table 5: Results of a generalised linear model (GLM) analysis showing the influence of distance from river and lagged monthly rainfall on the likelihood of the study pack crossing rivers in the Northern Tuli Game Reserve (NTGR) and Tuli Hunting Safari Block (THSB). Significance ($p < 0.05$) marked with *, significance ($p < 0.1$) marked with ·.

Distance from fence	Significant variables	P value	Beta estimate	Standard error
5 km	Distance from river	0.00506*	-0.44529	0.29104
	Lagged monthly rainfall	0.06033·	-0.8158	0.23706
10 km	Distance from river	1.17 e – 05*	-0.91395	0.20854
	Lagged monthly rainfall	0.00763*	-0.42923	0.16088

Due to the increased number of GPS locations utilised, only the results of the analysis which included all locations within 10 km of the rivers are shown below in figure 11.

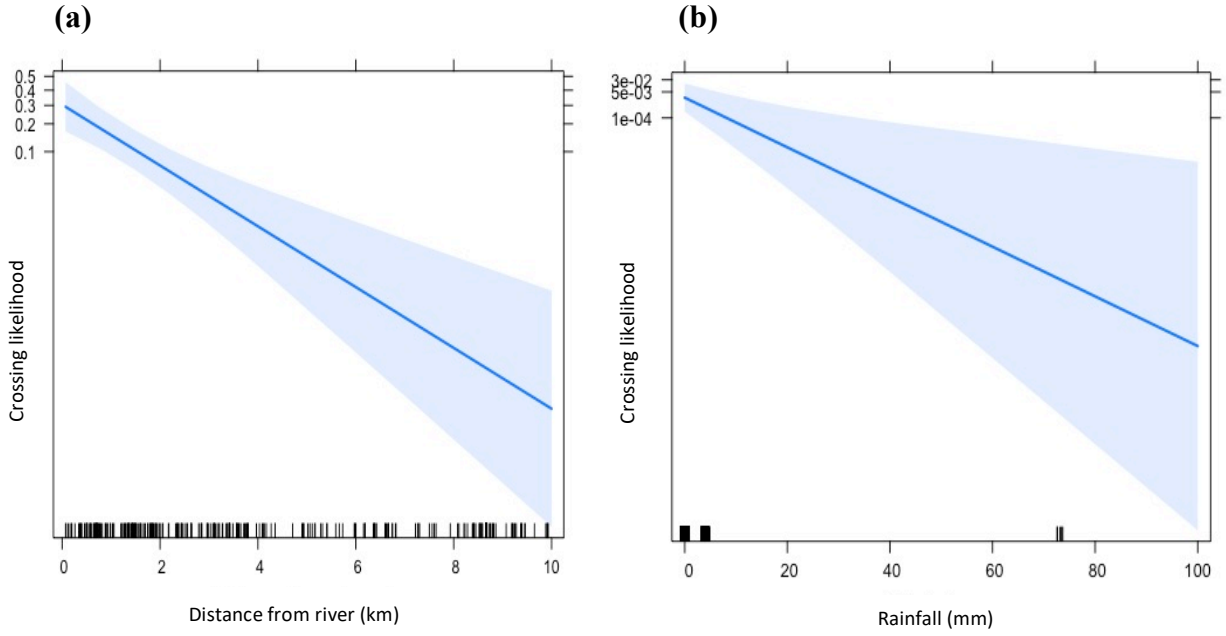


Figure 11: Likelihood of the study pack crossing a river within the Northern Tuli Game Reserve (NTGR) or the Tuli Hunting Safari Block (THSB) as a result of (a) distance from the river and (b) lagged total monthly rainfall when all GPS locations within 10 km of the rivers are included.

3.2.3 Barrier permeability

Within 1km of all barriers analysed, the predominant movement direction of the pack was parallel to the barrier (Appendix 4). Within 5km of all barriers analysed (aside from the Shashe river) the predominant movement direction of the pack was perpendicular away from the barrier (Appendix 4). Within 5km of the Shashe river, the predominant movement of the pack was parallel to this barrier (Appendix 4).

Shashe River

Movements with an easterly direction were considered perpendicular towards the Shashe river, those with a westerly direction were considered perpendicular away from the Shashe river. Movements with a northerly or southerly direction were considered parallel to the Shashe river. The predominant direction of movement within both 1km and 5km of the west bank of the Shashe river was southerly (Figure 12). A chi-squared goodness of fit test did not show any significant ($p < 0.05$) difference between the observed and expected results for the bearing categories within both 1 km ($p = 0.6055$) and 5 km ($p = 0.9214$) of the Shashe river.

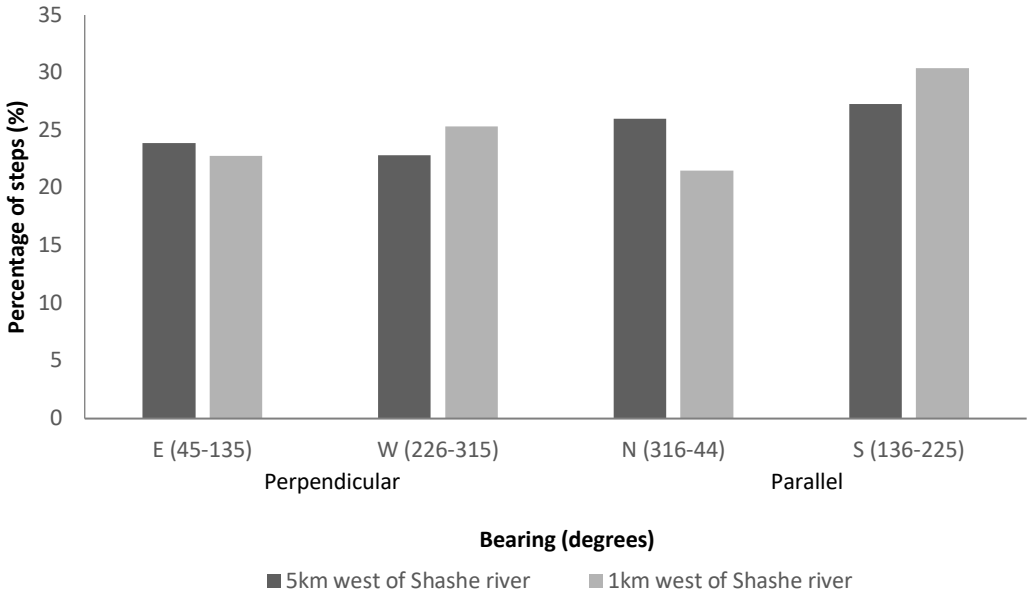


Figure 12: Comparison of the total steps of the study pack in the Northern Tuli Game Reserve (NTGR) and Tuli Hunting Safari Block (THSB) in each bearing category within 1 km and 5 km of the west bank of the Shashe river. Easterly movements were considered to show barrier permeability, all other movement directions were considered to show barrier impermeability.

Limpopo River

Movements with a northerly direction were considered perpendicular away from the Limpopo river, those with a southerly direction were considered perpendicular towards the Limpopo river. Movements with an easterly or westerly direction were considered parallel to the Limpopo river. The predominant direction of movement within 5km of the north bank of the Limpopo river was northerly, within 1km of this barrier the predominant direction of movement was westerly (Figure 13). The study pack was not recorded on the southern side of the Limpopo river during the nine months of the study. A chi-squared goodness of fit test showed no significant ($p < 0.05$) difference between the observed and expected distribution of steps within the four bearing categories within 5 km of the Limpopo river ($p = 0.1407$) (Figure 13). However, a significant ($p < 0.05$) difference was found between the observed and expected distribution of steps within the four bearing categories within 1 km of the Limpopo river ($p = 0.0001697$).

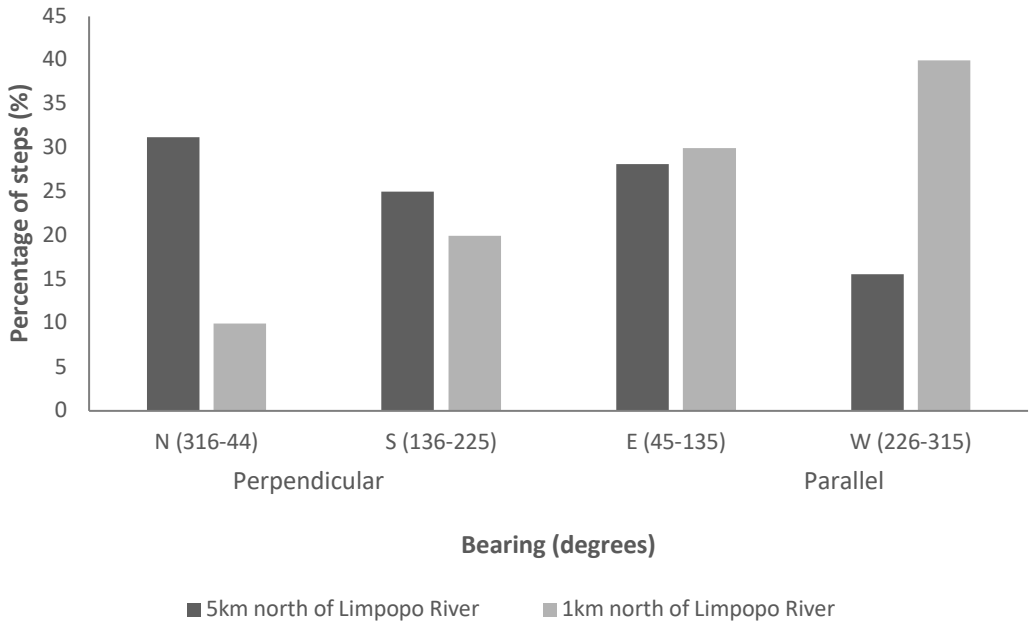


Figure 13: Comparison of the total steps of the study pack in the Northern Tuli Game Reserve (NTGR) in each bearing category within 1 km and 5 km of the north bank of the Limpopo River. Southerly movements were considered to show barrier permeability, all other movement directions were considered to show barrier impermeability.

Northern Tuli Game Reserve (NTGR) fence

Movements with an easterly direction were considered perpendicular away from the NTGR fence, those with a westerly direction were considered perpendicular towards the NTGR fence. Movements with a northerly or southerly direction were considered parallel to the NTGR fence. The predominant direction of movement within 5km of the east side of the NTGR fence was easterly, within 1km of this barrier the predominant direction of movement was southerly (Figure 14). There was only 4% difference between the bearing category containing the most and the category containing least steps within 5km of the NTGR fence (Figure 14). Indeed, within 1km the percentage difference between the bearing category containing the most and the least steps was even less (Figure 14). A chi-squared goodness of fit test showed that there was no significant ($p < 0.05$) difference between the expected and observed category totals within 5 km ($p = 0.9122$) and 1 km ($p = 0.9646$) of the fence.

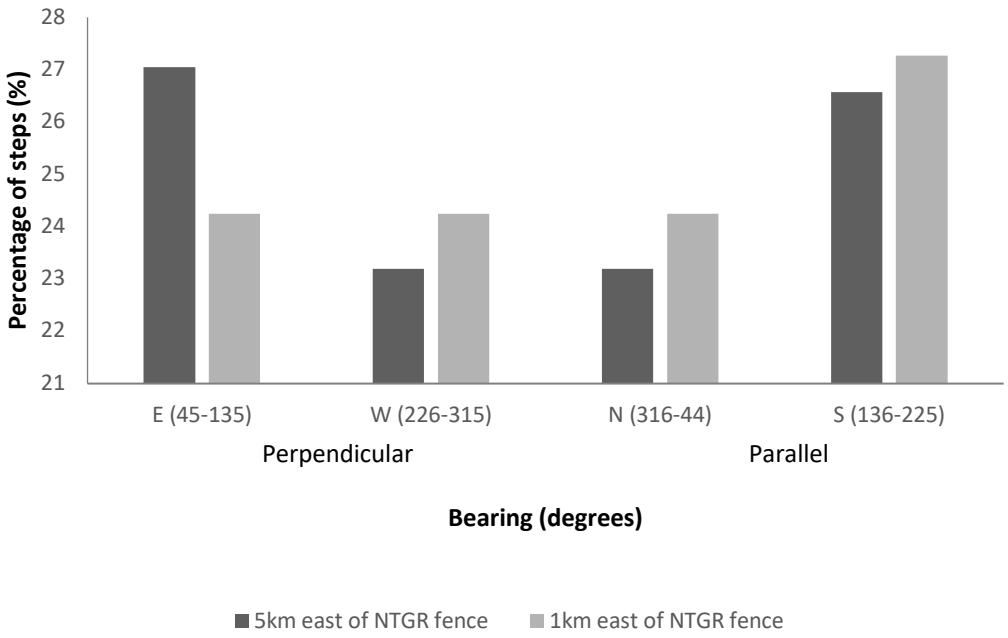


Figure 14: Comparison of the total steps of the study pack in the Northern Tuli Game Reserve (NTGR) in each bearing category within 1 km and 5 km of the east side of the NTGR fence. Westerly movements were considered to show barrier permeability, all other movement directions were considered to show barrier impermeability.

Foot and Mouth (FM) Fence

Movements with a northerly direction were considered perpendicular away from the FM fence, those with a southerly direction were considered perpendicular towards the FM fence. Movements with an easterly or westerly direction were considered parallel to the FM fence. The predominant direction of movement within 5km of the north side of the FM fence was easterly, within 1km of this barrier the predominant direction of movement was westerly (Figure 15). A chi-squared goodness of fit test showed no significant ($p < 0.05$) difference between the observed and expected totals of the bearing categories within both 5 km ($p = 0.6165$) and 1 km ($p = 0.1942$) of the fence.

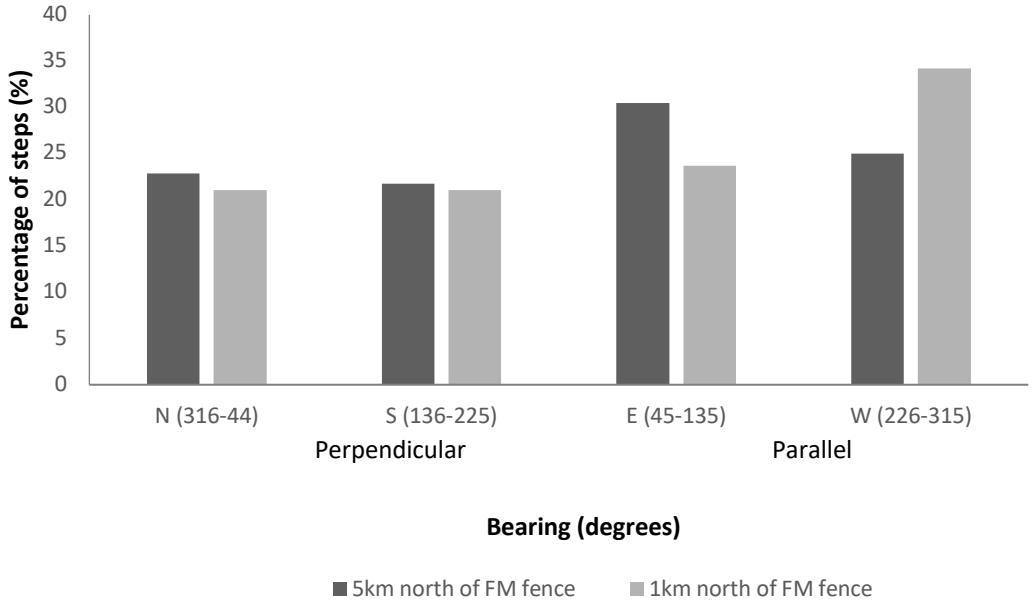


Figure 15: Comparison of the total steps of the study pack in the Northern Tuli Game Reserve (NTGR) in each bearing category within 1 km and 5 km of the north side of the Foot and Mouth (FM) fence. Southerly movements were considered to show barrier permeability, all other movement directions were considered to show barrier impermeability.

3.3 Resource utilisation

Beta (β) results from the resource utilisation functions showed that this pack of wild dogs demonstrates significant positive resource utilisation in sites further from rivers ($\beta \pm$ SE) (0.096 ± 0.033) with a higher terrain ruggedness index ($\beta \pm$ SE) (0.077 ± 0.025). The pack avoided areas with higher elevation ($\beta \pm$ SE) (-0.248 ± 0.036) (Figure 16).

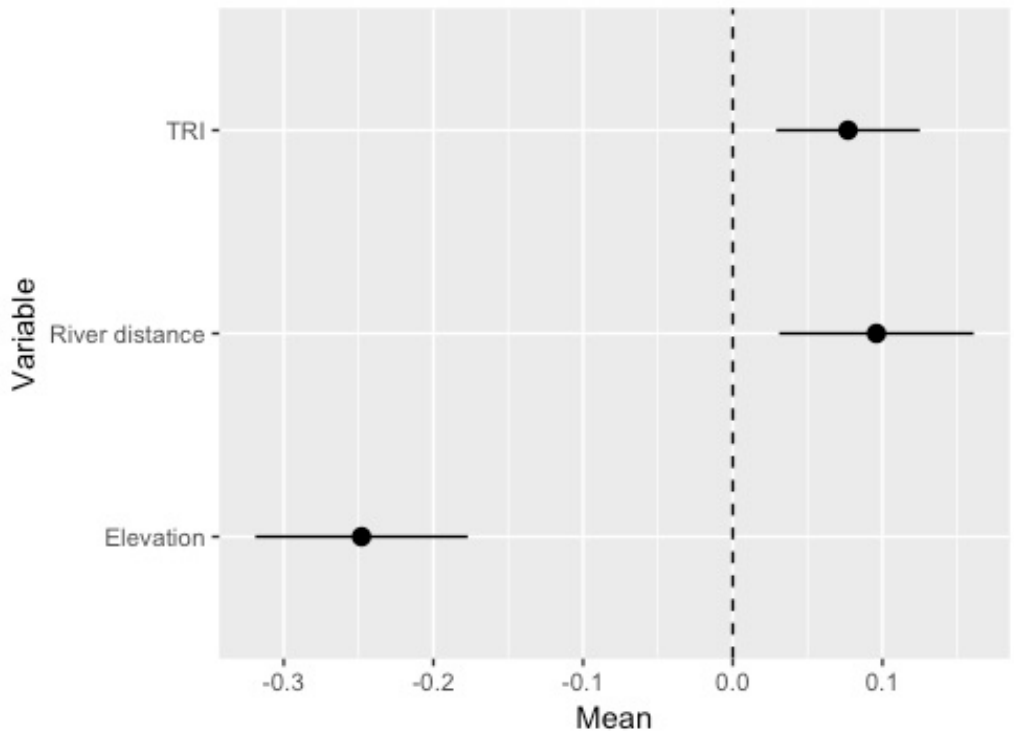


Figure 16: Graphical representation of the resource utilisation function results for the study pack in the Northern Tuli Game Reserve (NTGR) and the Tuli Hunting Safari Block (THSB) including centre Beta value, lower 95% confidence interval and upper 95% confidence interval.

4. DISCUSSION

In this study, I have analysed the movements of one pack of African wild dogs which were released in to the NTGR in February 2017. Three analyses were carried out; home range analysis, habitat resistance analysis and resource utilisation analysis.

4.1 Home Range Analysis

100% MCPs, 95% KDEs and 50% KDEs were generated to show total area used, home range and home range core area respectively. Whilst the monthly 95% KDE estimations for this study were large, none exceed the total area of the NTGR (720 km^2) and the maximum monthly value of 715.85 km^2 falls within the range reported for other studies of wild dogs viz., 377 km^2 - 850 km^2 (Silva-Opps & Opps, 2011; Jenkins *et al.,* 2015; Pomilia *et al*., 2015). Many studies have found that reintroduced packs of African wild dogs occupy home ranges larger than the protected areas in to which they were introduced. This can potentially lead to human-wild dog conflict as reintroduced individuals may come in to contact with livestock living adjacent to protected areas (Silva-Opps & Opps, 2011; Jenkins *et al*., 2015). While four out of the nine monthly 100% MCP home range estimations did exceed the 720 km^2 of the reserve, it is well established that MCP estimations typically over-estimate the size of a home range.

Large, dynamic home ranges are considered to be a consequence of the African wild dog's wide-ranging nature and prey requirements, as well as a competition avoidance strategy (Gittleman & Harvey, 1982; Jenkins *et al.,* 2015; Pomilia *et al*., 2015). Both Jenkins *et al.* (2015) and Pomilia *et al.* (2015) have indicated that variation in home range size is a consequence of landscape and ecosystem changes between the wet and dry season as well as changes in pack requirements between the denning and non-denning season. Although this study did not encompass all of both the wet and dry seasons there was nevertheless a marked range of 605.03 km^2 in the 95% KDE results which may be explained by a denning event.

The denning season for African wild dogs is believed to be between May and June, however some packs in northern Botswana have been recorded to den later in this period towards the end of June and even into July (Mills *et al*., 1998; Pomilia *et al.*, 2015). Pomilia *et al.* (2015) found that the home range of a pack of African wild dogs in northern Botswana in the denning season was 27% of that of the non-denning season. The 100% MCP result for the period of May-June (month 4) in this study was only 32.55% of the average home range estimation. Moreover the 95% KDE result for month 4 was only 37.89% of the average estimation. Aside from all home range estimations of the first month after release (month 1), all home range estimations for the study pack for month 4 were consistently the smallest of the nine months studied here. When African wild dogs breed successfully their home

range and daily distance moved decrease in size for around three months (Jenkins *et al*., 2015; Pomilia *et al.,* 2015). The home range of this study's pack only decreased in size for one month, whilst their daily distance moved increased over the period in which the home range contracted. Observations from the field reveal that this pack attempted to den and breed during month 4, but that the attempt failed within a month (Snyman A., Pers comm. 2017).

Attempts to den and breed highlight the development of knowledge concerning the landscape of the NTGR. This is evidenced by an increasing overlap of monthly home ranges throughout the study, demonstrating that this pack is in the transitional phase from explorative to exploitative behaviours in the landscape (Nathan *et al.*, 2008; Spencer, 2012; Berger-Tal & Saltz, 2014).

4.2 Habitat Resistance Analysis

The IUCN (2012) have highlighted the importance of understanding how landscape features impact the movements of African wild dogs. Barrier effect, crossing likelihood and barrier permeability were all used to analyse habitat resistance for this pack. Cozzi *et al.* (2013) found that while fences were relatively permeable to a pack of African wild dogs in northern Botswana, rivers were almost completely impermeable. They found no significant difference in the total GPS locations on either side of fences, yet a highly significant difference in GPS locations on either side of rivers. Using similar analyses, my results support these findings with rivers being a more effective barrier to the pack's movements than fences. Thus, the majority of the pack's movements were either parallel to or perpendicular away from the rivers in the landscape. This result was particularly strong when the pack was within 1km of the Limpopo river which suggested the dogs perceived it as an impermeable barrier and adjusted their movement accordingly. By contrast, the more even distribution of steps in each bearing category close to fences supports the finding that fences are perceived as a more permeable barrier than rivers for this pack. Parallel movements of this pack along fence lines could indicate that this pack are searching for areas of weakness in fences to cross or they are utilising fences when hunting large prey (as shown by Van Dyk & Slotow, 2003). Importantly, despite fences being permeable, the pack seldom moved far beyond these edges possibly because of increased human disturbance and an abundance of natural prey within the NTGR.

Both distance from the river and lagged rainfall had a significant negative effect on the probability of crossing either river in the landscape. While the pack did cross the Shashe river a number of times there was no recorded crossing of the much wider Limpopo river. Cozzi *et al.* (2013) found that a pack of African wild dogs demonstrated the highest likelihood of crossing a river in the Okavango delta in Botswana in the driest year of their study. The first time the study pack crossed the Shashe river was during the dry season on 22nd May 2017. Both the Shashe river and the Limpopo river are

non-perennial, however the Shashe river is ephemeral and therefore has a much-reduced flow compared to the Limpopo river. This difference in flow rate could possibly make the Shashe river much easier to cross. Whilst river flow data was unavailable during this study, this finding in addition to the significantly negative effect of lagged rainfall on crossing likelihood supports the idea that rivers containing water represent the most impermeable barrier to African wild dogs.

An important caveat to the findings on barriers in this study is the potential impact of land use outside the protected area on the propensity of this pack to both cross barriers and penetrate into land beyond them. All four barriers analysed in this study mark the boundary between very different land uses of protected area and agriculture. This is not the case for many other protected areas in southern Africa (many rivers in Kruger National Park, South Africa separate continuous sections of protected area) and therefore the land use difference could feasibly have a particularly strong, yet unproven effect on general habitat resistance (Snyman A., Pers comm, 2018).

4.3 Resource Utilisation Analysis

Van Dyk & Slotow (2003), Jackson *et al.* (2014), Jenkins *et al.* (2015) and Whittington-Jones *et al.* (2015) all found that African wild dogs utilise non-riverine areas with rough and rocky terrains. Evidence from the literature suggests that wild dogs actively chose these terrains to avoid competition and mortality from larger predators in the landscape such as lions (Van Dyk & Slotow, 2003; Jackson *et al*., 2014). My results support these studies with this pack utilising sites far from rivers, with low elevation, characterised by rugged terrain. Interestingly, Snyman (2016) ran a similar resource utilisation analysis for lions in the NTGR and found that they use sites close to riverine areas, with low elevation and a less rugged terrain. This suggests that the study pack is potentially selecting habitats to actively avoid predation risk and competition with lions. Such a finding reinforces the low permeability of large open river areas to this pack. Obtaining data surrounding the movement of lions and spotted hyenas in the NTGR over the same time period of this study would be valuable in any attempts to support or refute the development of a competition refuge by this pack (Jackson *et al.,* 2014).

A limitation of the current analyses is that there is no spatial information concerning human and livestock presence. Data on the distribution of human settlements, human and livestock activity and road density may all be important predictors of home range, habitat resistance and resource utilisation for the pack and are at this stage unknown but predicted to be important. Humans will influence the pack's movement directly through settlement development and habitat destruction and indirectly through the impacts on conspecific species. Lastly, it is possible that the increasing overlap in the location of monthly 95% KDE home range estimations in months 6 to 9 (early July to late October)

was influenced by an unidentified pack in the south of the NTGR that was observed on 9th May 2017 (Snyman A. Pers comm. 2017). This is likely to have resulted in the study pack moving away from this area to avoid intraspecific competition (Jackson *et al.,* 2014).

4.4 Management Implications

This study analysed the movements of only one pack of African wild dogs in a single area which limits the generality of the findings. However, the value of the study lies in the addition of a case study to existing data from African wild dog metapopulation reintroductions which can be used to derive consensus on best practice for successful reintroductions and increase the ability to predict movement patterns and hence possible conflict areas following reintroduction.

The results of this study support those of many others which demonstrate that in future reintroductions, this species requires a large protected area, with a heterogeneous landscape, preferably bordered by flowing rivers to restrict movement into agricultural land. However, whilst release site selection is important for reintroductions, the eventual aim of African wild dog conservation should be human-wild dog conflict reduction and mitigation, not only with a focus upon education but more importantly the amelioration of socio-economic conditions for communities surrounding reintroduction sites (Mills *et al.,* 1998; Gusset *et al.,* 2008). Studies have shown that educating farming communities surrounding protected areas in Botswana on the benefits of certain livestock husbandry methods such as kraaling can significantly reduce livestock predation events, in turn reducing conflict. Specifically, education regarding African wild dog ecology and the importance of this species for Botswana and its economic development have been shown to be valuable in reducing retributive killing and conflict events. Furthermore, socio-economic improvements stemming from local employment in protected areas and community-based tourism are valuable in ensuring reduced human-wildlife conflict. Compensation schemes are a commonly suggested method of conflict mitigation in Botswana; however, these have often proved to be ineffective as many report that the application process for compensation is overly complex and when applications are submitted applicants never receive their due compensation (Gusset *et al.,* 2009; Fraser-Celin *et al.,* 2017).

This study's findings can contribute to local human-wild dog conflict mitigation through highlighting potential sites of contact and conflict between humans, their livestock and this introduced pack. By mitigating conflict and focussing on education now, it is possible to allow for future reintroductions of African wild dogs in the NTGR. However, managers should take care to ensure that education and mitigation programmes have been successful before future reintroductions are considered, in order to prevent the loss of further African wild dogs to human-carnivore conflict (Van Wieren, 2012; Fraser-Celin *et al.,* 2017). Managers should also ensure that the home range of this study's pack has

stabilised spatially in the non-denning season prior to introducing a new pack to avoid territorial conflict and potential range expansion outside of the NTGR, generating further human-wild dog conflict.

The study as a whole is limited by a lack of time since release and observational data from the field. Longer term data could provide more reliable estimations of home ranges and resources selected and allow the inclusion of a climatic, seasonal effect on home range estimations. Observations from the field could be used to understand how the pack behaves when approaching major rivers and identify a wider set of variables (including those concerning human influences) which would allow for more detailed RUF results.

The death of one individual from the pack, alongside the failed denning attempt prevents this reintroduction from being termed a complete success yet (Gusset, 2009; Lewis *et al.*, 2012). However, it could be argued that the persistence of the pack in the landscape for almost a year would qualify the reintroduction as a partial success at this stage (Griffith *et al.,* 1989; Gusset *et al.,* 2008).

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6. APPENDICES

Appendix 1: Research Permit

TELEPHONE: 3914955
TELEGRAMS: MEWT
TELEX:
TELEFAX: 3914861
REFERENCE: EWT 8/36/4 XXXIII (56)

REPUBLIC OF BOTSWANA

MINISTRY OF ENVIRONMENT,
WILDLIFE AND TOURISM
PRIVATE BAG BO 199
GABORONE
BOTSWANA

ALL CORRESPONDENCE MUST BE ADDRESSED TO
THE PERMANENT SECRETARY

2 December 2015

Andrei Snyman
P O Box 26
Lentswe Le Moriti
Botswana

Email: andrei.synman@gmail.com

APPLICATION FOR EXTENSION OF A RESEARCH PERMIT:
NORTHERN TULI PREDATOR RESEARCH PROJECT:
EWT 8/36/4 XXXIII (48)

Your request for an extension to the above permit received on the 18 November 2015 refers.

Approval is given for extension of your permit from the **1st February 2016** up to **31st December 2018**.

Please note that the conditions of the above permit still apply.

Thank you

Yours Faithfully

G. Tapeng

FOR/PERMANENT SECRETARY

cc. Director, Department of Wildlife and National Parks

***Our mission**: To protect the environment; Conserve the country's renewable and natural resources; Derive value out of environment for the benefit of Botswana*

BOTSWANA
our pride, your destination

Appendix 2: Table of UDOI results for comparison months.

Table: Utilisation distribution overlap index (UDOI) results for consecutive monthly 95% kernel density home range estimations (KDE) for the study pack. Values close to 1 indicate complete overlap, values close to 0 indicate no overlap.

Comparison months	UDOI result
1-2	0.210
2-3	0.517
3-4	0.099
4-5	0.746
5-6	0.630
6-7	0.856
7-8	0.939
8-9	0.715

Appendix 3: Table of average monthly daily distance moved

Table: The average monthly daily distance moved by the study pack.

Dates in 2017	Month	N of GPS locations	Average daily distance moved (km)
16/02 – 15/03	1	125	4.44
16/03 – 12/04	2	103	5.22
13/04– 10/05	3	101	6.64
11/05 - 07/06	4	107	7.72
08/06 – 05/07	5	96	8.51
06/07 – 02/08	6	99	10.87
03/08 – 30/08	7	101	12.04
31/08 – 27/09	8	100	10.26
28/09 – 25/10	9	103	9.65

Appendix 4: Table of barrier permeability analysis results

Table: Results of barrier permeability analysis showing the average bearing of steps of the study pack in the Northern Tuli Game Reserve (NTGR) and Tuli Hunting Safari Block (THSB) within 1 km and 5 km of the barriers. The bearing category containing the most steps within 1 km and 5 km of the barriers is also shown.

Barrier	1 km average bearing	1 km category	5 km average bearing	5 km category
NTGR fence	177.10°	Parallel	168.07°	Away
FM fence	178.69°	Parallel	146.75°	Away
Shashe river	181.84°	Parallel	191.57°	Parallel
Limpopo river	210.58°	Parallel	141.49°	Away